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A Reconstruction of Animal Classification	*J. Hadži*	145
Comparative Ethology of Spider Wasps	*H. E. Evans*	155
Variation in Opiliones	*C. J. and M. L. Goodnight*	173
Plant Taxonomy Today	*R. C. Rollins*	180
Points of View: Uniform Endings	*G. B. Moment*	191

Index for Volume 2 (1953)

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Systematic Zoology

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An Attempt to Reconstruct the System of Animal Classification

J. HADŽI

THE conservative attitude of most zoologists toward any fundamental change in the system of animal classification is to a certain extent understandable in view of the great divergency in such attempts. Moreover, any major change entails obvious practical complications. But every open-minded zoologist is aware that the constant growth of knowledge of the natural history of animals must lead occasionally to a revision of the prevalent system.

Important discoveries in the field of general zoology lead to changes in the system of classification. I should like to mention especially the thorough changes in our ideas concerning the relationship between ontogeny and phylogeny or between "embryos and ancestors" as put forward by de Beer, a subject to which Garstang especially contributed. The interpretation of these relationships has played a great part in the construction of the system of animal classification ever since the time of Haeckel. At that time, however, too much support was sought from morphology and embryology, while the ecology and physiology of animals were given too little consideration. Thus it happened that primitive characters were confused with characters secondarily simplified either by sessile habits or by parasitic life, and that the phenomena of symmetry were incorrectly interpreted. For example, the Radiata were regarded as a phylogenetically uniform group, but it has long been quite certain that radial symmetry has developed in many lines as a consequence of transition from free life to a sessile existence.

The Position of "Coelenterata"

Exaggerated conservatism coupled with a blind veneration of authority has been responsible for the persistence of Haeckel's interpretation of the position of the so-called Coelenterata or Diploblastica. This group was assigned to a most important position in the phylogenetic system, that of the transition from Protozoa to Metazoa. In accordance with Haeckel's ideas it was generally assumed that the Coelenterata developed from flagellate colonies as small, two-layered saccules along a hypothetical path represented by the sequence: blastea—morea—gastrea. Consequently the Coelenterata were placed at the base of the Metazoa. The triploblastic Coelomata were supposed to have developed from the Coelenterata. For this reason it was at one time customary to subdivide the Metazoa into Coelenterata and Coelomata or into Radiata and Bilateria. Fortunately it was early realized that genetically the sponges have nothing in common with the Coelenterata. Much later the Ctenophora, which show some similarity to the Cnidaria owing to convergence caused by their planktonic type of life, were removed from the Coelenterata (Hadži, 1923) because it was shown that these bisymmetric animals developed by neoteny from planktonic larvae of Polyclada.

Thus, as the only representatives of the supposedly primitive Coelenterata, the Cnidaria alone were antithetic to the much larger group of Coelomata. At first there was no objection to the long-accepted idea that the Cnidaria represent a long, progressively developed series. The Hy-

drozoa with the simplest structure, solitary polyps such as *Protohydra* and the legendary *Hydra,* were always placed at the bottom of the system. It seemed to be quite natural to assume that the Scyphozoa, which show a much more complex organization, developed from the more primitive Hydrozoa, and that the Anthozoa, which are the most highly organized Cnidaria, developed from the Scyphozoa. Therefore it appeared quite reasonable to place these three classes in that sequence in the system of classification.

It was completely ignored that the polyps, from which the medusa stage had secondarily developed, are sessile; and the generally prevailing rule that sessile animals develop not progressively but regressively, at least in so far as their organization is concerned, was quite forgotten. Paleontologists were the first to point out that the Anthozoa, which were regarded as the most highly developed Cnidaria, exhibit distinct traces of bilateral symmetry (Schindewolf, Kühn), and that this fact is at variance with the commonly accepted interpretation of the nature of Cnidaria. After forty years of intensive research on the so-called Coelenterata, I arrived at the conclusion that the nature of the Cnidaria is misunderstood. In a book published in 1944 I showed that the radially symmetric polyp stage of Cnidaria is only the result of a secondarily acquired habit of sessile life and that the evolution of Cnidaria is chiefly regressive. Therefore the Anthozoa are in reality the original group of Cnidaria, from which the Scyphozoa and then the Hydrozoa developed. Lack of space prevents my giving here a more detailed exposition and references necessary for support of my thesis concerning the origin of the simpler Cnidaria. These may be found in my original publication and also in several later ones. Here I shall restrict myself to a few important points.

Sessile and, therefore, radially symmetric Cnidaria must be derived from bilaterally symmetric animals which led a free life and possessed free locomotion. Having produced a polyp form as a consequence of sessile life, the ancestors of the Recent Cnidaria lost all systems of organs, organs which were of use to them while they were endowed with free locomotion. The protonephridial system disappeared completely. The nervous system became greatly reduced, the nerve centers disappeared, and only nerve plexuses remained. Complex sense organs were lost. The muscular system became so reduced that it was finally restricted to only two intercrossing layers of muscular prolongations of ectodermal and endodermal epithelial cells. The digestive tract was gradually simplified. In the anthopolyps an ectodermal gullet is still present and the digestive tube forms strong longitudinal folds. The scyphopolyps and the hydropolyps have no gullet and the wall of the digestive cavity of the hydropolyps is quite smooth. All accessory organs of the reproductive system have disappeared and only isolated groups of reproductive cells are left, located either under the ectodermal layer or under the endoderm.

Generally speaking, the middle layer or mesoderm underwent a very considerable reduction. I prefer to call this layer the *mesohyl.* At the extreme end of its evolution, as for example in *Protohydra* and *Hydra,* the mesohyl as a distinct layer has altogether disappeared. Only remnants of it in the shape of so-called *I*-cells remain between the bases of the ectodermal and endodermal cells, while the acellular interstitial lamella has assumed the function of an internal skeleton.

I should like to add that the Anthozoa possess no medusa stage, and that at present only in the Anthozoa do solitary polyps of primary nature occur. Scyphozoa and Hydrozoa developed a medusa stage independently while their polyps became sessile and asexual. Among the Hydrozoa the highest point of specialization was reached by the Siphonophora, which are secondarily planktonic and have developed polymorphism of individual polyps among true colonies. And just as in some species of Bryozoa (*Mono-*

bryozoon ambulans Remane) solitary individuals were secondarily produced, so some Hydrozoa, and *Hydra* among them, became again solitary polyps.

As in the case of parasites a progressive development of some organs goes along with the reduction of other organs, so a connection existed in Cnidaria between their development and their sessile mode of life. The strongly contractile organs for the capture of prey developed into tentacles into which diverticles of the digestive system extended. Out of simple glandular cells which possessed the capacity for producing a partially solid secretion, through considerable qualitative and quantitative changes nettle cells or cnidae developed to which these animals owe their name Cnidaria. The highest degree of this development was attained by the Hydrozoa in the "batteries" of the Siphonophores. In this order several differentiated types of nettle cells are transported in a complicated way from the place of their origin to the place in the body of the colony where they are to be used.

Now that we have shown that the phylogenetic development of the Cnidaria was chiefly regressive, from the Anthozoa to the Scyphozoa and finally to the Hydrozoa, in consequence of a secondarily acquired type of sessile life, the next problems arise: first, the question as to the animal type from which the Cnidaria derived, and second, how this affects their position in the system of animal classification.

If we base our study upon comparative anatomy with due regard for ecological facts, then we shall easily realize that the ancestral type and the nearest relatives of the Cnidaria are to be sought and found among the Turbellaria. Among recent Turbellaria the Rhabdocoela seem to be the nearest relatives of the ancestors of Anthozoa. This is indicated by a whole series of characters, of which only the following need be mentioned: the ciliated epithelium, the ectodermal glandular cells with a partially solidified secretion as a first step in the formation of cnidae, a digestive system with an ectodermal gullet and a tendency to produce folds and diverticles, the possession of tentacles, the formation of a nerve net.

In this connection I should like to remind the reader of the fact that the Cnidaria have often been regarded as relatives of the Turbellaria, but that their relationship was interpreted in a reverse direction, just as within the group of the Cnidaria themselves the Hydrozoa were considered to be the most primitive members. According to our interpretation the Cnidaria are Turbellaria which became polyp-like and therefore also radially symmetrical. Something similar (though in a lesser degree, because they are phylogenetically younger) happened to the Temnocephala among the Turbellaria and to the Camptozoa (Entoprocta) among the Ameria Euprocta.

Thus the position of the Cnidaria in the system of animal classification becomes correctly defined: they do not occupy a position at the base of the Eumetazoa as an independent type, but form a branch near the base of the stem which is represented by the Turbellaria (Fig. 1). The Ctenophora also form a branch of the Turbellaria, originating at the place occupied by the Polyclada. The Turbellaria prove thus to be a centrally situated type of primarily unsegmented Eumetazoa from which a great number of subordinate types have developed. Therefore they play a role of the first importance in the phylogeny of Eumetazoa.

For many years the Turbellaria have been regarded as the most primitive Protostomia or Triploblastica, and quite correctly so, although they possess an exceedingly complicated hermaphroditic sexual system. (This complexity is now easier to understand, as will be shown below.) In this connection two questions arise: which is the most primitive subgroup of Turbellaria, and with which group of Protozoa should it be related?

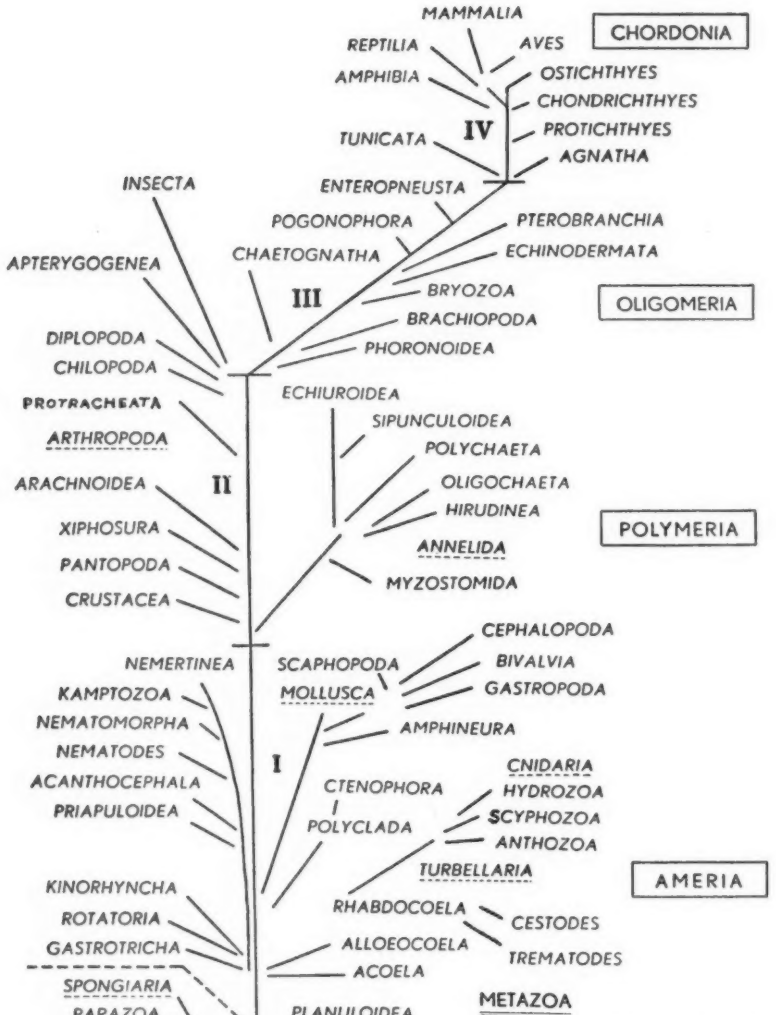

FIG. 1. Diagram depicting the relations between animal groups in the form of a phylogenetic tree.

The Origin of Turbellaria

It is quite obvious that the Acoela are the simplest Turbellaria. Many zoologists, among them specialists in Turbellaria, consider that the Acoela are secondarily simplified animals, that is, that they are Turbellaria which underwent retrogressive development. This view is quite wrong because the Acoela are neither sessile nor parasitic. It is true that they are small and that a decrease in size is often coupled with a reduction in the complexity of organization. But with few, evidently secondary exceptions, Turbellaria are generally primitive animals of small size. I feel quite certain that the Acoela are truly the most primitive Turbellaria because with their predaceous type of life they show clear traces of a progressive development, especially in the case of their reproductive system (Beklemischev, 1944). The primitive nature of the Acoela is attested by all their organ systems.

Greater difficulties seem to arise when one attempts to establish a connection between the Acoela and the Protozoa. Turbellaria have been compared with Infusoria at various times, and an impressive number of striking resemblances between them has been pointed out. But such similarities were always regarded as mere analogies, as meaningless coincidences which have nothing to do with the problem of phylogeny. The way to a true interpretation was blocked by the current idea that all Metazoa developed from *Volvox*-like flagellate ancestral stems. The so-called biogenetic law of Haeckel, or the theory of recapitulation, with reference to the common stages of early ontogenetic development (oöcyte, total segmentation, morula, blastula, and gastrula), excluded the possibility of a derivation of Eumetazoa from any infusorian-like ancestor.

However, if we give a correct interpretation today to the relationship "embryos: ancestors" (de Beer, 1951), then we come to the conclusion that it is much more probable that Eumetazoa were produced, not by an integration of originally independent unicellular individuals, but from Protozoa through a polymerization of organelles, including the nucleus. Such polymerization had already played an important role in the Protozoa and led to the development of Polymastigina and Hypermastigina, and from them finally to Infusoria.

In the light of a correct interpretation of the relationship "embryo: ancestor" the striking similarities between Infusoria and Acoela become clearly understandable. Many years ago the opinion was expressed that Eumetazoa originated from multinucleate Protozoa. The present types of Infusoria, which are mostly binucleate with a distinct morphological and physiological dimorphism of nuclei, cannot be regarded as ancestors of Turbellaria. A process of cellularization must have followed upon a multinucleate stage. Thus the ancestral Eumetazoa must have inherited from their protozoon ancestors differentiations already acquired by the latter, along with a unity of the individual retained by them. The important process of cellularization which permitted an increase in the size of the body must have been slow and, especially in the mesohyl (the middle layer), remained incomplete even at the highest pinnacles of evolution. There always remained smaller or larger portions of the eumetazoan body in which multinuclearity persisted as an inheritance from infusorian ancestors or appeared as a throwback. Among the primarily primitive Acoela there still exist today species in which the process of cellularization has affected little more than the reproductive cells and the skin; the middle layer and the digestive inner layer still retain the multinucleate condition.

A more comprehensive comparison, in the light of the idea here presented for a derivation of Turbellaria from Infusoria-like ancestors, shows us step by step that the respective structural parts of both animal types are not only outwardly similar but in reality homologous. This applies especially to the three somatic layers,

so that the problem of the mesoderm and of its origin, as well as that of the coelom, is placed in a totally new light. The protonephridia, whose origin has posed such a problem (let us recall only the attempt to interpret them as indrawn combplates of ctenophores) can now be quite simply derived from the pulsating vacuoles of Infusoria, situated in the middle layer, just as the digestive system of Turbellaria can be derived from the digestive vacuoles of the fluid inner layer.

I cannot go further into particulars in the present paper, but one seemingly insurmountable difficulty in the way of such derivation must be given consideration. It has to do with the sex conditions which at first glance are so fundamentally different in Infusoria and Turbellaria. The sexual phase has undergone considerable specialization in Recent Infusoria, but this may be derived from the conditions typical in other Protozoa. Thus conjugation may be interpreted as modified copulation. First of all it is characteristic of Infusoria that they do not produce a generation of free gametes and that the number of gametes reduced to mere karyonts has been restricted to the lowest hermaphroditic value, i.e. to a single pair. The act of conjugation must be interpreted as the pairing of two hermaphroditic gamonts each with a single gynegametic or androgametic karyont. In the process of pairing, a cytoplasmic bridge is formed through which both androgametes pass in the shape of karyonts and fertilize the gynegametes which are in the state of stationary karyonts. The zygote itself remains inside the body of the infusorian individual, which now enters upon its vegetative stage, loses its former vegetative nucleus (macronucleus), and produces by division a set of nuclei for a new generation.

The Turbellaria are also hermaphroditic and reproduce by pairing. Fertilization in them is therefore also internal, but no cytoplasmic bridge is formed, because in their case special organs of copulation have been developed. The reproductive cells, greatly increased in number, become cellularized like many other somatic cells. They become typical gonads of both sexes producing typical androgametes (sperm) and gynegametes (eggs). Naturally, since the time of separation of the ancestral Turbellaria from the ancestral Infusoria, both groups continued to develop along divergent lines.

This radical change in the point of view regarding the probable origin of the Eumetazoa involves certain far-reaching consequences which are in a general way important in systematics. The first of these consequences is that the customary subdivision into Coelenterata and Coelomata must be discarded as superfluous, because primarily diploblastic Eumetazoa do not exist at all. A distinction between Bilateralia and Radiata is useless for a separation of large groups as has long been felt, because Eumetazoa which possess a primarily radial symmetry do not exist.

Two Lines or One?

What must be done now is to show what conception one has of the phylogeny of the Eumetazoa that would provide a foundation for a systematic arrangement of groups. Most authorities are of the opinion that the phyletic development of large groups (phyla) proceeded in two parallel lines. One of these lines is termed Protostomia and the other Deuterostomia, following Hatschek and Grobben. This division is based chiefly on certain facts of ontogeny, such as the formation of the mouth opening and of the coelomic mesoderm, and is responsible for the alternative names, Ecterocoelia and Enterocoelia, for these two lines. According to different authors this bifurcation in the mode of development occurred at different times and is correspondingly represented in their systems. Some would have it occurring very early and at a low level of organization, while according to others the division came much later and at a higher level.

But if one arranges the classification of

animals in a system, primarily on the basis of comparative anatomical evidence furnished by fully developed individuals, taking into account their way of life and using ontogeny with circumspect criticism, one comes to the conclusion that there is no binding reason for the existence of such a bifurcation. This becomes especially evident when one considers anew the matter of the coelomic mesohyl. It then appears to be much more probable that the development of the Eumetazoa progressed in the main along a single line, i.e. that the so-called Deuterostomia or Enterocoelia may be derived from the higher Protostomia or Ecterocoelia. This occurred when the fully segmented Annelida underwent a strong regressive reduction in consequence of their change into organisms less capable of locomotion, which lived in tubes or in the soft deposits at the bottom of the sea. Thus an oligomeric type was produced in a natural way through regressive development of a polymeric type. Once the division of the system of classification into Protostomia and Deuterostomia is abolished, it becomes possible to simplify it without exaggerated schematization. This is particularly valuable inasmuch as it reduces the need for systematic categories of an order higher than phyla. (See Pearse's "List of Phyla, Classes and Orders," especially where it deals with Coelenterata and Platyhelminthes.)

Origins of Coelomic Spaces

Before I present my own division into phyla I should like to return to the question of the coelom because the coelom and the middle somatic layer in which the coelomic cavities appear have always played a major role in the main division of animal types. Zoologists differ greatly in their opinions concerning the so-called mesoderm, and still more so concerning the coelomic cavities which appear in it. From the point of view of the turbellarian theory of the origin of Cnidaria and of the derivation of Eumetazoa from Infusoria-like ancestors, all these relationships appear not only considerably simpler, but also much more uniform, thus giving a far more convincing aspect to the fundamental systematic divisions.

From this point of view, as we have seen, the middle somatic layer does not represent a completely new acquisition of the Eumetazoa at the time of their change from Diploblastica to Triploblastica. On the contrary, it was transmitted by the protozoan ancestors to the ancestral Turbellaria in the shape of a subcortical cytoplasmic layer together with the fluid-filled clefts and cavities in it. Among them were already present pulsating vacuoles, or emunctories. In the cytoplasm itself there were present various fibrillar structures, contractile, nervous, and elastic. This layer, the mesohyl or the mesoderm, retained most tenaciously its multinucleate, syncytial state even when, at a still later period, it underwent considerable differentiation into muscular, nervous, and connective tissue.

The first system to develop from clefts and cavities was the nephridial system, when the clefts changed into protonephridia and the cavities into nephrocoels by becoming lined with mesohyl cells arranged into epithelia. Clefts and cavities lacking an epithelial lining may be regarded as primary body cavities, and those with a lining as secondary body cavities. Coelomic cavities are present everywhere, either where fluids are in rhythmic or often repeated motion, flowing or peristaltic, or where solid parts move in respect to one another (blood, lymph, secretions, excretions). Consequently there must be several coelomic systems. A unique system of organs which may acquire a cavity is represented by the gonads with their gonocoel. But it would be quite misleading to attempt a derivation of all true coelomic cavities from this quite special type.

As the next coelom formation after the nephrocoel, the haemocoel appears in the form of a blood-vessel system in the nemerteans. Isolated cases of special cavi-

ties are found among the "lower" Eumetazoa, for example, the rhynchocoelom of the nemerteans and the pericardial coelom of the Mollusca. Among the "lower" Eumetazoa the Mollusca occupy the highest position inasmuch as they possess concurrently several coelomic cavities, but not the one which is generally spoken of as the "true" coelom and which I shall call the perigastrocoel. In the higher Eumetazoa the perigastrocoel plays a very important morphogenetic role.

The perigastrocoel or true coelom originated presumably at the time of the change of "lower" (i.e. primarily unsegmented) Eumetazoa into segmented Eumetazoa. It appeared at first as a cleft in the mesohyl along the digestive tube, which was endowed with peristaltic motion within an elongated body with snake-like locomotion. As in the case of other coelomic spaces, this cleft enlarged to the size of a cavity and was lined with an epithelium. Since there are no known animals now living with a primarily unsegmented (i.e. a common) perigastrocoel, the conclusion is permissible that the gastrocoel was at its very beginning segmented. It follows from this that a wide gap must be seen as separating segmented from unsegmented Eumetazoa. This was recognized years ago by Bütschli, who called all primarily unsegmented Eumetazoa Ameria. Naturally the Mollusca also belong to the very large group of Ameria, because there is no reason to consider them as being secondarily unsegmented (in the tetrabranchiate Cephalopoda there is evidently a partial duplication of organs present). We are quite justified in giving the group of Ameria the rank of a phylum.

Numerous zoologists attach to the group of "lower worms" transitional types of poorly segmented Eumetazoa (Acoelomata of Pearse, Pseudocoelomata of Schimkevitch), which were given different names (Vermidia, Tentaculata) and embraced somewhat wider or narrower groups (including or excluding the Echinodermata, etc.). Such treatment of the Oligomeria must be definitely opposed because all these types of animals show easily recognizable traces of regressive development clearly connected with their mode of life, for they all possess a more or less pronounced polyp form. The only ones among them that show a progressive tendency are those which have secondarily returned to free locomotion, among them the Chaetognatha and especially the Echinodermata, and in a lesser degree the Enteropneusta. To place the so-called Entoprocta or better Camptozoa (Cori) in the Oligomeria, as Pearse does, is not correct. The Camptozoa are quite typical primarily unsegmented animals which became sessile; they belong without any doubt to the Ameria.

In the phylum Polymeria the perigastric coelom had undergone diverse modifications, not only in fully developed animals, but also in the process of its formation in the course of ontogeny. The anlage of the coelomic portion of the mesohyl was early separated from the anlage of the non-epithelial portion (the so-called mesenchyme) and the anlages of the nephridia and the gonads. Admittedly the mesoderm proper originates in the Annelida as a pair of primordial mesodermal cells. They come to lie at the borderline between the skin anlage and the digestive tract anlage, for which reason the group was most unfortunately termed Ecterocoelia. In connection with the formation of a larval type (trochophora) leading a planktonic life, the manner of the development of the perigastrocoelic mesohyl was so modified that the paired coelomic sacs are formed in two series. In the first series only a few pairs of the "larval mesoderm" or larvatum of Schulze are formed, while the remaining numerous pairs develop subsequently during metamorphosis (Ivanow). The perigastrocoel became connected with the polymerized nephridia, giving origin to metanephridia. A direct connection between the coelom sacs and the gonads was also established.

In the higher Polymeria, the Arthro-

poda, because of a changed mode of life and the appearance of appendages, the body length was shortened and the coelom sacs were resorbed. This had already happened independently and partially in the Hirudinea among the Annelida. Thus a myxocoel was produced and only the pericardium remained as a remnant of the original coelomic system. The manner of the formation of the mesohyl was consequently modified in the ontogenesis of the respective groups.

Of greater importance in general for the phylogenetic development is another modification of the Polymeria. Among the Annelida some of the Chaetopoda gave up the mode of life with free locomotion. We find already in tubicolous Polychaeta a strong tendency toward the reduction of coelomic sacs through a disappearance of the dissepimenta. This process goes still further in species which live in fissures of rocks or in the soft bottom deposits of the sea (Echiuroidea, Sipunculoidea). They show traces of the polypoidal form in the shape of a ring of oral tentacles. Here is a quite natural link with typical oligomeric forms (Phoronoidea and Pogonophora which are still tubicolous, and Enteropneusta which burrows in soft sand), and further between the totally sessile Brachiopoda and Bryozoa, and Pterobranchia and Echinodermata. The regression of the perigastric coelom system is accompanied by a considerable change in the formation of the anlage in ontogenesis. This anlage was shifted to the dorsal side of the embryo and was thus brought into closer relationship with the anlage of the gut. Too much importance was attributed to this change, and the opposition of the Ecterocoelia to the Enterocoelia was used for the separation of large phyletic groups. But the shift was in reality not quite so sudden. We find that the enterocoelic type of formation has already occurred in the Ecterocoelia, i.e. Protostomia, as for example in Tardigrada (Pearse places them strangely in the superphylum Aschelminthes). The enterocoelic condition was retained also by the last-evolved phylum, Chordonia; that is, it was firmly anchored in ontogenetic morphogenesis.

The strong reduction of polymerization which not only involved the segmentation of the body, but also led to the formation of a polyp form characteristic for all semisessile and sessile animals, was at least in two instances overcome within the oligomeric type. This happened first in the Echinodermata, which changed to a freely mobile but crawling type of life with the aid of ambulacral tubes. Their polymerization with the fundamental number of five antimeres did not, however, involve as usual the perigastric coelom system, because it was developed in a plane almost transverse to the main axis of the body. The second time, polymerization appeared in the Enteropneusta in a way similar to that in nemerteans. Here too, it did not involve the perigastric coelom system. Thus we find in different groups of oligomeres many characters or traces which, when combined with an extension of the body in the course of the transition toward a more active mode of locomotion, led to the production of an important new type of structure, that characteristic of Chordonia.

The ancestral Chordonia inherited from their oligomeric ancestors the gill slits of the foregut, the dorsal nerve chord, the enterocoel, and the tendency to polymerization in the metasoma and to the formation of an inner skeleton out of a mesenchymatic connective tissue. To this was added as an innovation a new postanal section of the body in the form of a muscular tail, and a tendency to metamerization arising from that of the somatic muscles. Thus the series of the major animal types was completed.

Conclusions

We have arrived at the construction of a natural system of animal classification (Fig. 1) which I believe is in better agreement with modern knowledge. This has been achieved, not by trying to find at

any cost, for didactic or other subordinate reasons, a simplification and equalizing of the classification, but rather by founding the scheme primarily on comparative anatomical facts, starting with the theory of the turbellarian origin of Cnidaria and taking into account and correctly interpreting the facts of ontogeny and ecology. If we disregard the Protozoa, which must still wait on expert treatment, as well as the Mesozoa and the Parazoa, and consider only the Eumetazoa, then we come to the realization that only four large animal groups should receive the rank of phyla, arranged one after another in a straight-line series: Ameria—Polymeria—Oligomeria—Chordonia. Within this series, which in general is progressive, one period of regression took place in the case of the Oligomeria. Naturally, while the Oligomeria were, because of their mode of life, undergoing regressive development, other groups previously classed as phyla but actually belonging to the other three here-recognized phyla, such as Mollusca among the Ameria and Arthropoda among the Polymeria, continued their progressive development.

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SYSTEMATIC ZOOLOGY is privileged to be able to introduce to an English-speaking audience **JOVAN HADŽI**, whose stimulating and thought-provoking views on animal phylogeny may well cause us to re-examine the system so generally accepted today. Dr. Hadži, a member of the Yugoslavian National Academy, is Professor of Zoology at the University of Ljubljana. This manuscript was prepared specially for SYSTEMATIC ZOOLOGY and obligingly translated from the German by Dr. Alexander Petrunkevitch.

Comparative Ethology and the Systematics of Spider Wasps

HOWARD ENSIGN EVANS

COMPARATIVE anatomy has always been the major wellspring of taxonomic data. For practical reasons it probably will always remain so. A curator cannot be expected to identify and arrange his collections on the basis of chromosome number, serum agglutinations, and behavior during courtship. "Keys" will always be important by-products of taxonomic investigations, and keys must always be based largely on morphological characters, preferably external ones. But they are only by-products. In his studies of the natural relationships of organisms and in his attempts to interpret the patterns of evolution within groups, the systematist must avail himself of all possible sources of data. Once he has arrived at certain conclusions, it may then be possible to re-evaluate the morphological characters in such a way as to present a key which will be useful and yet far more meaningful than one compiled hurriedly for purposes of identification. If this is not possible, progress has still been made toward a classification which more nearly approximates the ideal, even though it may still be necessary to depend upon artificial keys for identifying specimens.

The inconvenience of using ethological characters in classification is obvious: one must work with living specimens in their normal habitat or under conditions closely resembling their normal habitat. It would be impossible to maintain, however, that behavioral characters are less "important" than structural characters; indeed, it would be easier to maintain that the reverse were true. It has been stated recently that "biological characters are of paramount importance to the classifier, for habits and behavior are certainly deeply rooted and are often the product of a very ancient evolution" (Delacour and Mayr, 1945, p. 49). In his admirable essay on "The Comparative Method in Studying Innate Behaviour Patterns," Lorenz (1950, pp. 239–240) states:

> Though I emphatically deny the charge that comparative morphology is a spent science which has already borne all its fruits, I should concede that it certainly has borne the most important of them. . . . Phyletic comparison is slow and painful work, even in morphology, where the comparable, homologous characters are immediately and permanently accessible to the anatomist's knife. It is obvious how the difficulties are increased in the study of innate behaviour patterns which are not there continuously, just to be looked at and described, but for which one must wait in patient observation. . . . The immense field of observation which is still waiting to be systematically exploited needs whole armies of investigators.

Recent Literature

Perhaps more progress in comparative ethology has been made in the birds than in any other group of animals. The great attractiveness of birds to students of natural history and the rather obvious differences in song, courtship, nesting, and other activities among various species have resulted in the accumulation of a considerable mass of data on life histories and behavior. Only recently, however, have ornithologists begun to avail themselves of the possibilities of utilizing these data taxonomically. In 1911, Herrick proposed a classification of the nests of birds and studied the variation in the nests of certain species. Nest characters have occasionally been used in considering the classification of certain groups of birds; for example, Mayr and Bond (1943) made

much use of nesting behavior in their "Notes on the Generic Classification of the Swallows." Behavior patterns associated with courtship and mating have also been used in bird systematics. Stonor (1936) used the displays of male birds of paradise in discussing the relationships and phylogeny of six species of Paradiseidae. In a study of the grouse family (Tetraonidae), Wing (1946) compared in tabular form seven genera with respect to various aspects of the behavior of courtship, and presented a phylogenetic tree based on these characters. In his excellent book *Bird Display and Behaviour* (1947), Armstrong saw fit to include a chapter on "The Comparative Study of Display." Virtually all aspects of behavior were investigated by Hinde (1952) in his ethological study of the genus *Parus* (Paridae); the greatest differences between the species of this genus were found in song and in feeding behavior.

Perhaps the most complete studies of bird behavior have been made on the ducks and geese (Anatidae). Heinroth (1911) was the first to point out the value of ethological characters in this group, and his work served to stimulate a number of other workers, particularly Lorenz and Delacour, who both kept ducks and studied their habits in detail. The classification of waterfowl had been based in the past on a limited number of morphological features, and many workers were aware of its serious shortcomings. Lorenz has published several papers dealing with the Anatidae, and in one of his more recent ones (1941) presents a detailed account of the display of numerous species and uses behavioral criteria in a reconsideration of the phylogeny of the family. In 1945, Delacour and Mayr presented a reclassification of the Anatidae which made full use of the relatively extensive ethological data. By employing both behavioral and structural characters, they were able to arrive at a far more satisfactory classification than had previously been possible. They believe that in some cases displays afford better evidence on relationships than morphology or color patterns. The work of Delacour and Mayr stands as a model of the successful application of comparative ethological data in taxonomy, and their paper has done much to stimulate further work along these lines in other groups of birds.

The phylum Arthropoda presents more unsolved taxonomic problems than any other, if only because of its great size. All arthropods exhibit instinctive behavior of varying degrees of complexity, and because of the abundance of species and individuals would seem to provide excellent subjects for comparative studies. Workers on spiders have made much use of behavioral characters ever since the pioneering work of McCook (1889–94) on spinning habits and of the Peckhams (1889, 1890) on courtship and display. Petrunkevitch's stimulating paper "The Value of Instinct as a Taxonomic Character in Spiders" (1926*a*) is well known. Kaston in "The Spiders of Connecticut" (1948) makes frequent mention of behavioral differences and presents two excellent plates (108 and 109) showing different positions during copulation. A most outstanding series of research papers dealing with the comparative biology of Venezuelan jumping spiders (Salticidae) has been published by Crane (1948–49). Part IV of this study presents a fascinating analysis of display, including phylogenetic considerations based on dependence on chemical stimuli, display criteria, and method of locomotion. An additional paper in this series, dealing with the correlation of ethological with morphological characters, is promised.

Even the Crustacea provide excellent subjects for comparative studies of behavior, as Crane showed in an earlier paper on fiddler crabs of the genus *Uca* (1941). It was found that each species studied had a

> definite, individual display, differing so markedly from that of every other species observed, that closely related species could be recognized at a distance merely by the form of the display. Furthermore, related species had

fundamental similarities of display in common, and series of species, showing progressive specializations of structure, in general showed similar progression in display.

Recently Crane (1952) has undertaken a comparative study of innate defense behavior in 15 species of Trinidad mantids (Insecta: Orthoptera). Four types of defense mechanisms were found in these insects: protective resemblance (including twig and leaf mimicry), active escape, startle display, and aggressive attack. The first two were found to occur in all the species studied, though never in identical form, while the last two occurred only in some of the more specialized forms. Startle display was analyzed into various behavioral components, which are discussed from an evolutionary standpoint. The survival value of the various defense mechanisms is pointed out, and several experiments along these lines are described. Of special interest is her study of the ontogenetic development of behavioral traits in several of the species.

In his studies of termites, Emerson has several times pointed out the importance of ethological characters. In his paper "Termite Nests—A Study in the Phylogeny of Behavior" (1938), several interesting points are made. First, he points out that "nest structures are morphological expressions of behavior patterns. This quality makes aspects of behavioral evolution as visible as morphological evolution and similar principles and terms may be directly applied." The nests of social insects, he further points out, are not the work of single individuals, but of many hundreds of individuals of closely similar behavioral constitution. Another point made by Emerson is that the higher categories of classification seem far less arbitrary than some authors would have us believe when morphological characters are supplemented by behavioral, physiological, and ecological criteria.

Several recent articles illustrate the value of ethological characters in revealing "cryptic" species of insects, that is, species which had not been separable by ordinary taxonomic procedures. Fulton (1952) in North Carolina has made a study of field crickets, hitherto considered a single species on morphological grounds. By using characters such as song, seasonal cycle, and habitat, he has been able to discern four populations. In breeding experiments, no successful crosses were obtained between members of different populations. Thus there appear to be four species involved, although further study failed to reveal any structural features by which they can be separated. In a fascinating study of the firefly genus *Photuris*, the late H. S. Barber (1951) was able to separate 18 species and subspecies where only four had previously been recognized; 12 of these he described as new. The major criteria used were various details of the courtship behavior, particularly the duration, interval, and color of the flashes of the males. Barber presents a table in which 16 forms are compared with respect to various characteristics of the flashes. Flash characters are employed in the keys, although for the most part they have been supported by minor differences in size, color, and structure. Barber's research was conducted on only one genus and in only a few localities, and one wonders what may lie in store for future students of the Lampyridae who follow Barber's leads.

Students of the dipterous genus *Drosophila* have been aware for some years that these insects possess a distinct courtship which differs in details among different species of the genus. This was nowhere more clearly brought out than by Spieth (1947) in his study of the mating behavior of six species of the *willistoni* group. Presenting his results partly in tabular form, allowing ready comparison of the species with respect to each element of the behavior, Spieth demonstrated that differences exist in the posturing of the male, the signifying of acceptance by the female, and the nature and duration of copulation. He concludes: "These differences roughly parallel the morphological differences that exist between the species. . . . Thus the

evolution of the sexual behavior has approximated quantitatively the evolution of the morphological characters." More recently (1952) Spieth has performed an invaluable service by bringing together available information on the entire genus *Drosophila*. He finds the validity of recent divisions of the genus into subgenera and species-groups to be substantiated on the whole by behavioral studies. His table 2 (pp. 413–414) summarizes graphically data on the mating behavior of 101 species and subspecies of *Drosophila*. Spieth's paper is one of the most important contributions to biology in recent years, and these few lines can by no means do it justice.

The Hymenoptera offer a tremendously rich field for studies in comparative behavior. Many writers have commented on the fixity of instincts in various species of wasps, bees, and ants. Even Linnaeus saw fit to include a few ethological notes in his descriptions of several of these insects. In the last century a host of workers have published observations on the habits of the higher Hymenoptera, the most notable being Fabre, Forel, Ferton, Adlerz, Nielsen, Peckham and Peckham, Rau, Williams, Claude-Joseph, Iwata, and others. In spite of this, it is only rarely that hymenopterists have had available sufficient ethological data on which to base many conclusions. An excellent example of the possibilities, however, is provided by Ducke's classic study of the classification and phylogeny of the social Vespidae (1913), in which he makes extensive use of nesting behavior. The books of Wheeler (1923, 1928) have done much to stimulate work in this field. Plath (1934) proposed a classification of bumblebees based on certain aspects of the nesting behavior, and Duncan (1939) has indicated the close parallel between morphological and biological characters in defining the genera of hornets and yellow-jackets. Nielsen's splendid monograph on the biology of *Epibembex rostrata* (1945) includes much comparative data on the various genera and species of Bembicini (Sphecidae). Spooner, in his recent study of the British species of psenine wasps (Sphecidae) (1948), has compiled the available ethological data on these wasps and has found clear-cut generic and some specific differences. In a newly published paper, Linsley, MacSwain, and Smith (1952) present a biological study of the bee *Diadasia consociata* and proceed to discuss the comparative ethology of certain groups of Anthophoridae. If these recent papers are indicative of present trends among hymenopterists, the outlook is most encouraging.

Particular note should be made of the recent work of several European authors on digger wasps of the genus *Ammophila* (=*Sphex* of most American authors). Baerends' wonderfully detailed and carefully analyzed studies of the nesting and orientation of *"Ammophila campestris"* (1941) are already a classic of their kind. Studies by Adriaanse (1944, 1947) indicated to him that *A. campestris* in the sense of various authors was divisible into two behavioral types, which he called *A* and *B*. Wasps of the two types differ in their manner of opening and of filling and covering the burrow, in their choice of prey, and particularly in the fact that *A* completes the provisioning of one nest before starting a second, while *B* ordinarily digs one or two additional burrows for future use while still provisioning the first. After the discovery of these behavioral differences, Wilcke (1945) found morphological differences which enabled him to describe type *B* as a new species, *A. adriaansei*. Baerends' studies apply to *adriaansei*, while the earlier studies of Grandi, Maneval, and others apply to the true *campestris*. It would be difficult to find a more trenchant example than this of the importance of ethological studies in systematics.

The preceding discussion does not pretend to cover all the literature, or even all the important literature, in the field of comparative ethology and systematics. Nor does the material which follows pretend to serve as a particularly striking

example of the use of this method. There are far too many serious gaps in our knowledge of the biology of spider wasps, and there are very few sufficiently detailed studies of individual species. Nevertheless, the subject is one which has interested the writer for several years and on which he is doing further work at present. The purpose of this paper is not to present any specific conclusions, but rather to illustrate the application of comparative ethology to the study of this group. In the following presentation I have made use of the published observations of a host of workers, and have also borrowed freely from the ideas presented in the excellent syntheses of Nielsen (1932), Richards and Hamm (1939), and Iwata (1942).

An Ethological Characterization of the Pompilidae

On morphological grounds, the Pompilidae are very distinctly set off from other wasps, so much so that a recent catalog of the Hymenoptera (Muesebeck and others, 1951) declined to place the family in any of the major superfamilies. Some authors, such as Wheeler (1928), have recognized a special superfamily for this family. On the basis of behavior, spider wasps are scarcely less distinctive. The following combination of behavioral characters will define the family as clearly as any comparable set of morphological characters. (1) All utilize spiders as larval food. One or two records of their using Orthoptera are of doubtful authenticity; one record of their using phalangids (Evans, 1948) is scarcely adequate to erase the generalization. A number of non-pompilid wasps, of course, also utilize spiders, including our common mud-daubers. (2) All stock the nest-cell with a single paralyzed prey, thus limiting the larva to a single host specimen. Among other wasps, this habit is exhibited principally by certain Scolioidea and Bethyloidea. A few members of the family Sphecidae also use a single host per cell. (3) In transportation to the nest, the spider is seized in the wasp's mandibles and dragged backward over the ground. Some Bethylidae and Ampulicidae exhibit this behavior, and numerous Pompilidae depart from it to a greater or lesser extent. (4) The apex of the abdomen of the female wasp is used as a tool for pounding down the earth when closing the nest or, in mud-users, as a trowel for manipulating the mud. The use of the tip of the abdomen for pounding the earth has been described by numerous authors; this habit is also exhibited by many Sphecidae, although the Sphecinae use the head for this purpose. The use of the abdomen as a trowel has also been described by several authors, but especially by Williams (1919), who points out that other mud-daubers use the mandibles and legs for this purpose.

Another characteristic (5) I add somewhat cautiously, since there seem to be many exceptions to it. This is the habit of preparing the nest after the prey has been taken, the spider being deposited nearby while the nest is dug. A number of authors have cited this behavior as being specially characteristic of Pompilidae, and it is true that the vast majority seem to follow this sequence, as do many Bethylidae. The great bulk of the Aculeata, however, prepare the nest first and then seek the prey. This permits the storage of several specimens for larval consumption; it also permits, as a further advance, progressive provisioning of the larva; ultimately it may result in contact between offspring and adult, and the origin of an insect society. The sequence of prey → nest or nest → prey may thus explain why social forms have arisen among the Vespoidea and Sphecoidea-Apoidea stocks, but not among the Pompilidae. It is significant that some of the more highly evolved, mud-building Pompilidae, which prepare the nest first, have become subsocial (Williams, 1919).

It is true that no one of these characteristics is in itself absolutely distinctive, but the same would be found true of a similar listing of morphological charac-

ters. Single characters are, in any event, of little significance by themselves, but only as units in a combination of characters. On morphological grounds, it is not easy to deduce the correct phylogenetic position of the Pompilidae. On ethological grounds, the conclusion seems inescapable that they were derived from bethyloid-scolioid stock and have evolved independently of other stocks of aculeates. Ethologically, they could easily be derived from the Bethylidae, but structural differences forbid relating them to any existing bethylid. In any event, it is of considerable interest to trace the possible evolution of the behavior patterns of Pompilidae from those of primitive Hymenoptera, and to attempt to understand the major ethological types which occur among these wasps.

The Development of Ethological Types within the Pompilidae

It is generally held that the Aculeata were derived from some ancient stock of Terebrantia or "parasitic Hymenoptera." The Ichneumonoidea most closely approximate such a stock, and it is here that we must begin our analysis. In many ichneumons the adult female, following mating, seeks a host upon which to lay her egg; the egg is generally laid singly and externally, the resulting larva feeding externally. This behavior consists, then, of only two major steps: Hunting → Oviposition (VO).[1] These are, of course, repeated several times in the life of the insect. A few Ichneumonidae, such as the genus *Polysphincta*, sting their prey into temporary paralysis before oviposition, thus introducing a third step: Hunting → Paralysis → Oviposition (VPO) (Type 1 of Iwata, 1942; Type I of Nielsen, 1932). This is the sequence of behavior in many primitive Aculeata, for example, in most Bethylidae and Tiphiidae.

Of great interest is the habit of certain wasps of the family Scoliidae of reorienting or actually moving their prey following stinging and before oviposition. These wasps, finding their white grub prey on or just beneath the surface of the soil, may burrow to a considerable depth, dragging the grub behind them, finally laying their egg on it deep in the ground. Thus a fourth step is introduced: transportation. Paralysis in this case is generally permanent. A number of Bethylidae paralyze their caterpillars and then drag them to some suitable cavity. The four steps of this behavior are then: Hunting → Paralysis → Transportation → Oviposition (VPTO) (Type 2 of Iwata, 1942).

An apparently minor variation of this, but one of perhaps considerable phylogenetic importance, is the habit of some wasps of covering their prey once it is placed in some cavity and an egg laid upon it. This involves a fifth step: Hunting → Paralysis → Transportation → Oviposition → Closing (VPTOC) (Type 3 of Iwata, 1942; Type II of Nielsen, 1932). Wasps of the family Ampulicidae exhibit this type, as do a considerable number of Pompilidae. For example, the pompilid *Agenioideus cinctellus* (Spinola) is known to place its prey in old bee tunnels, crevices in walls, snail shells, etc.; following oviposition, the nest-cell is closed over with debris (Richards and Hamm, 1939). The common American *Priocnemis cornica* (Say) uses various holes in the ground, usually old tiger-beetle holes, which it later plugs with earth (Rau and Rau, 1918, and observations of author). Some species of *Priocnemis, Anoplius, Dipogon,* and other genera, not infrequently modify the cell-hole in various ways, and may return to the same general cavity for further cells. These forms grade imper-

[1] Iwata (1942) has invented the very useful practice of indicating the steps in the behavior by the use of abbreviations. I have used Iwata's system in this paper, and feel that it merits wider application in studies of the Hymenoptera. His abbreviations are as follows:

C — *Claudere,* to close the cell
I — *Instruere,* to prepare the nest-cell
O — *Ovum parere,* to lay the egg
P — *Pungere,* to sting the prey
T — *Transferre,* to carry the prey
V — *Venari,* to hunt

ceptibly into the next two ethological types, which are characterized by the actual construction of a nest.

The vast majority of Pompilidae belong to ethological type VPTIOC: Hunting → Paralysis → Transportation → Excavation of cell → Oviposition → Closing (Type 4 of Iwata, 1942; Type III of Nielsen, 1932). Iwata indicates 46 species belonging to 15 genera as exhibiting this type of behavior. Most genera of Pompilini fall here (*Pompilus, Anoplius, Episyron, Tachypompilus, Aporinellus,* etc.) (see Evans, 1951–52). In the Pepsini, *Calicurgus* and some species of *Pepsis,* at least, come in this group. A few of these merely modify some pre-existing cavity, but most of them actually construct a burrow in the soil with a terminal cell (often selecting a depression or crevice as a starting-point). Type VPTIOC is highly characteristic of the Pompilidae, and only a few other wasps exhibit it (e.g., *Prionony*x in the Sphecidae).

The next step involves no additional behavioral elements, but does involve a fundamental transposition: the nest is constructed first, and then the hunting begins and the other activities follow in the usual order (IVPTOC) (Type 5 of Iwata, 1942). A good example is the common European species *Pompilus plumbeus* Fabricius, as described by a number of workers (though this species seems to be an exception within its genus). Many of the forms belonging here build several cells from a common burrow. *Priocnemis exaltatus* (Fabr.), a common European species, is described by Adlerz (1903) as preparing several cells from a common gallery, and Claude-Joseph (1930) records similar behavior for two Chilean species of *"Salius"* (*Priocnemioides?*). Members of the genus *Dipogon* should probably be classed here; these are not diggers, but seek out an empty beetle gallery in wood, or a hollow stem, and proceed to make a series of nest-cells which are separated by barriers of mud, plant fibers, or other materials (Iwata, 1942; Richards and Hamm, 1939). The habit of building multicellular nests seems especially prevalent in the Pepsini, though it is by no means characteristic of the entire tribe. The habit of bulding or finding the nest before hunting the prey is, in general, not widespread in the Pompilidae, though it is the usual sequence in the sphecoid and the vespoid wasps.

Forming a special group undoubtedly arising from the preceding type are most members of the tribe Auplopodini (Macromerini of some authors), which actually construct a nest-cell out of mud, plant resins, or other materials. The details of behavior in constructing such a nest are vastly different from those involved in digging one in the soil, and this element in the behavior might thus be designated as I′, and the whole ethological type as I′VPTOC. The nests of these "mud-daubing" pompilids have been described by many authors; several different types are described and illustrated by Williams (1919). Although only one spider is placed in a cell, several cells are commonly built in close proximity. According to Williams, *Macromeris* will guard its nest fearlessly, remain with it for some time, and actually use some of the cells a second time. In the genus *Paragenia,* Williams has noted that several females may share a single nesting cavity and actually exhibit some co-operation. The development of a subsocial habit such as this was possible only after the reversal of sequence occurring between types VPTIOC and IVPTOC.

In this analysis, then, the Pompilidae embrace ethological types VPTOC (primitive), VPTIOC (basic), and IVPTOC and I′VPTOC (specialized), these being traceable back to primitive Hymenoptera by way of types VPTO, VPO, and VO. It should be pointed out that these have been selected for present purposes from the great number of ethological types occurring in the higher Hymenoptera as a whole. The inclusion of the vespoid and sphecoid wasps, the bees, the ants, or the more specialized parasitoids, would involve a great many types, some of them fairly complex and more difficult to trace than the seven steps which carry us

through the Pompilidae. Nevertheless, even in the relatively generalized family of spider wasps, there are certain genera which cannot be placed in any of the types described above, and for which certain special ones must be recognized.

First of all, there are certain genera of cleptoparasites[2] such as *Evagetes* and *Ceropales*. The female *Evagetes*[3] enters the freshly provisioned nest of an *Anoplius* (or certain other genera), destroys the egg which is on the spider, and lays one of its own; the *Evagetes* larva then devours the spider laboriously captured and interred by the *Anoplius*. Here the hunting phase of the behavior has been much modified: the wasp walks over the ground seeking not an active spider (which it will ignore) but one already paralyzed, placed in a cell, and bearing an egg. It is capable of doing whatever digging is necessary to reach the cell, and leaves the nest more or less closed on departure. Thus its behavior might be described as V′IOC, the host supplying PT (type IV of Nielsen, 1932). This apparent simplification of behavior is suggestive of the structural simplification generally characteristic of parasites. A more extreme example is provided by *Ceropales*, whose behavioral type might be indicated simply V′O′. The hunting activities of *Ceropales* are directed toward finding another spider wasp in the process of nesting and *before* the spider is interred; the egg is inserted inside the booklungs of the spider, where it will not be detected nor harmed during its interment; the egg of the host is laid on the spider in the usual manner, but the *Ceropales* egg hatches first and the larva destroys that of the host, then feeds upon the spider (Adlerz, 1902). The Oriental genus *Xanthampulex* apparently has much the same habits as *Ceropales* (Williams, 1919).

A second group of genera also show progressive reduction in their behavior patterns, but here an entirely different phenomenon is operative. These genera (structurally very diverse) have opportunistically omitted certain steps in their behavior, resulting in a return to simpler types of behavior. For example, Williams (1928) has vividly described the habits of *Aporus hirsutus* (Banks), a California species which preys on the trap-door spider *Aptostichus*. After ingeniously luring the spider from its burrow, the wasp pursues it and stings it, then drags it back to the original burrow of the spider, lays an egg upon it, and closes over the burrow. The European *Pompilus* (*Anoplochares*) *spissus* Schiødte, according to Adlerz (1910), enters the burrow of certain species of *Tarantula*, stings the spider, lays its egg, then leaves and closes over the entrance; the spider is lightly paralyzed and remains somewhat active. The behavior of *Psorthaspis*, which preys upon trap-door spiders (Jenks, 1938), and of *Notocyphus*, which preys upon arboreal nest-building spiders (Williams, 1928), is essentially similar. The behavior-type of *Aporus* is thus VPTOC; that of *Anoplochares*, *Psorthaspis*, and *Notocyphus* is VPOC. In the usual economy of nature, elements which no longer serve a purpose have been lost.

Some suggestion of the probable origin of this type of behavior may be found in such a species as *Anoplius marginalis* (Banks). This species has a well-developed tarsal comb and has been regarded as a typical fossorial species (VPTIOC). The Raus (1918, pp. 45–58) found this species preying upon *Lycosa* and *Pellenes* and constructing a nest in the soil. The author has found this species nesting in the soil of a Kansas corn field and using *Lycosa baltimoriana* Keys. as prey (un-

[2] Also variously called cuckoos, social parasites, and labor-parasites (*Arbeitsparasiten*). To my mind the term cleptoparasite (Greek *kleptes*, thief) is the most descriptive of these. For a general discussion of this type of parasitism among the wasps, ants, and bees, see Wheeler's paper "The Parasitic Aculeata, a Study in Evolution" (1919).

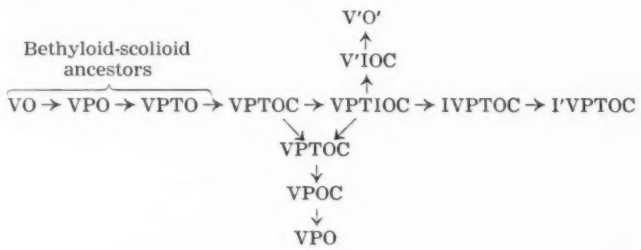
[3] The structural characters separating *Evagetes* from *Pompilus* are very slight, and the two groups have been much confused in the past. In recently redefining *Evagetes* in its present sense, the writer (Evans, 1950, p. 159) was strongly influenced by ethological characters. This reference also includes a brief review of the biology of the group.

published observations). However, Krombein (1953*a*) found this species attacking a burrowing spider, *Geolycosa pikei* (Marx), near the entrance of its burrow and later dragging the spider into its own burrow (VPTOC). On another occasion (1953*b*) he observed an *Anoplius marginalis* attacking this same species of spider *inside* its burrow; neither wasp nor spider emerged, and the wasp apparently was making use of the spider's burrow as a nest (VPOC). If this versatile wasp is able to omit unnecessary steps in its behavior, it is easy to see how a species which *specializes* in burrowing or nest-building spiders may have done the same in the course of its evolution. The species of *Aporus, Psorthaspis, Notocyphus,* and *Anoplochares* have lost the tarsal comb, and presumably would have difficulty in digging a hole of their own at the present time.

The greatest reduction in behavior occurs in the Old World genus *Homonotus.* These wasps attack spiders of the genus *Cheiracanthium,* which build nests by spinning together leaves and other bits of vegetation. After being attacked by the wasp, the spider recovers from the paralysis and goes about its normal activities until the wasp larva, developing like a parasitoid on its abdomen, finally kills it (see Richards and Hamm, 1939, p. 105). Thus there is no essential difference between the behavior of *Homonotus* and that of an ichneumonid such as *Polysphincta* (VPO). There is evidence that certain American genera have habits similar to *Homonotus.*

Iwata (1942) classes the genera mentioned above in his types 1 and 3, and Nielsen (1932) puts *Homonotus* in his type I, implying that these represent primitive types of behavior within the family. On the surface this might seem to be the case. My reasons for regarding this as a type of development specialized by reduction are three. (1) The genera belonging to this group are extremely diverse and all seem specialized structurally. (2) The fact that all of these forms appear to prey upon a specific type of spider with specialized habits suggests that the wasps themselves are specialized. (3) The steps in this particular chain are not precisely the same as those postulated earlier as the major line of ascent, using evidence from lower Hymenoptera (VPO → VPTO → VPTOC as against VPO ← VPOC ← VPTOC). It will be difficult to prove this particular point, however, unless some evidence of vestigial behavior indicating derivation from more complex types is found in such genera as *Homonotus or Psorthaspis.*

The probable development of various ethological types within the Pompilidae may be summarized as below. This should not be interpreted to mean that the genera belonging to any one behavior-type are necessarily derived from those in the preceding, but that the behavior-types themselves are so derived. *Ceropales* (type V′O′), for example, is clearly not a derivative of *Evagetes* (type V′IOC). What is meant is that at one time in its evolution *Ceropales* probably behaved very much as *Evagetes* does now.



Variation within Behavioral Units

The preceding discussion has concerned itself with the over-all sequence of behavioral units and has attempted to trace the gross behavior from the simple to the complex and, in some cases, back again to the simple, much as a morphologist might trace an organ system through a group of animals. Most of the higher categories in the Pompilidae can be characterized as exhibiting one (or two or more) of these ethological types, just as they may exhibit one or more stages in the development of certain body parts.

It should not be assumed, however, that all species exhibiting a certain ethological type have identical or even greatly similar behavior patterns. Variation may occur within any of the individual behavioral units. In so far as these differences are genetically determined and characteristic of populations, they provide an excellent source of taxonomic characters, especially on generic and specific levels. It may be worth while to consider certain of these possibilities at this point.

Hunting behavior has been little studied as such, although it is, of course, closely integrated with the habits of the spider being hunted, and considerable data on host selection are available. It seems probable that what is actually inherited is a series of responses *likely to lead* to the discovery of a certain host, rather than an innate ability to select or reject certain spiders, though the latter factor must certainly play a role in obtaining a spider of the right size. Thus spider wasps inhabiting a restricted ecological niche or possessing a specialized mode of hunting are likely to be more or less host-specific, while wide-ranging forms whose hunting behavior is plastic and unspecialized are likely to take a wide range of hosts. In the latter category might be mentioned such forms as *Priocnemis cornica* (Say), a widely distributed North American form which occurs in many different situations and which preys upon virtually any species of errant spider of proper size (Rau and Rau, 1918; observations of author). Some species of *Anoplius*, in particular, are exceedingly versatile with respect to their host. Richards and Hamm (1939, pp. 90–96) present a long list of known hosts for the European *A. fuscus* (Linnaeus); the list includes spiders belonging to five families.

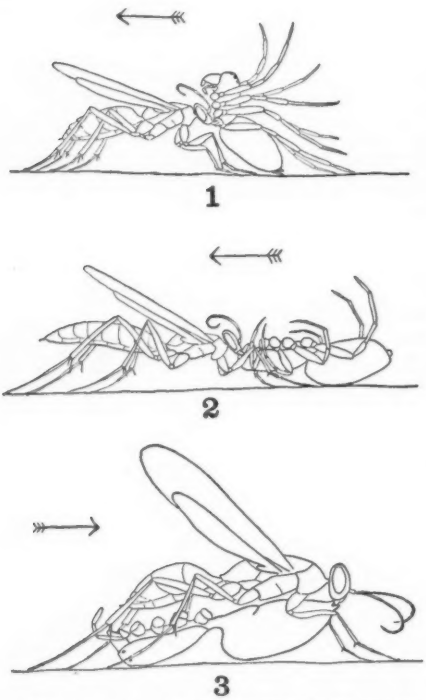
It is also apparent that some pompilids are more or less host-specific. For example, all records so far indicate a specificity for orb-weavers (Epeiridae) for the genera *Episyron, Batazonellus, Poecilopompilus,* and *Calicurgus. Pedinaspis, Aporus,* and *Psorthaspis* prey upon trap-door spiders (Ctenizidae); *Tachypompilus* on wolf spiders (Lycosidae); *Aporinellus* upon jumping spiders and crab spiders (Salticidae and Thomisidae). Obviously the details of behavior involved in capturing a trap-door spider are vastly different from those involved in capturing an orb-weaver (*cf.* Williams, 1919, p. 105 [*Batazonellus bioculatus* Bingham attacking an orb-weaver] and Williams, 1928, p. 135 [*Aporus hirsutus* Banks attacking a trap-door spider]). Apparently a few species of spider wasps are completely host-specific. Petrunkevitch (1926*b*) demonstrated that *Pepsis marginata* Beauvois is able to discriminate between species of spiders and uses only *Cyrtophilus portoricae* as prey in Puerto Rico. This author has recently (1952) made the statement that each species of *Pepsis* requires a certain species of tarantula, and that the wasp will not attack any other species. Judging from the review of the subject by Hurd (1952, pp. 265–270), however, it seems probable that some species of *Pepsis* are much less selective than *marginata* appears to be. Much work, both observational and experimental, needs to be done on this aspect of the behavior before it will be possible to draw many valid conclusions regarding the host specificity of various species and genera.

Even fewer comparative data are available with respect to the second unit of behavior, that of *paralyzing* the spider. The act of stinging, where it has been

carefully observed, seems to differ little within the family. It is well known that the sting of some species causes only a light and temporary paralysis, the spider remaining in the cell only because it is packed so tightly that it cannot dig its way out. This is the case in many species of *Anoplius*, for example, *A. nigerrimus* (Scopoli) (Richards and Hamm, 1939) and *A. apiculatus* (Smith) (Krombein, 1953*a*; Evans, Lin, and Yoshimoto, 1953). In other cases paralysis is profound and of long duration. Three spiders taken from *Sericopompilus apicalis* (Say) before oviposition remained alive for 18, 44, and 46 days, responding weakly to prodding but otherwise inert; the larva of this species requires only seven days to complete its feeding (unpublished observations of writer). Minkiewicz (1934) kept a spider stung by *Cryptocheilus affinis* (Van der Linden) alive for four months, and it never recovered fully from the paralysis. In some species the adult will feed on the spider briefly at the site of the puncture, or will chew the spider until it exudes some blood, which is lapped up. Of particular interest is the habit of most Auplopodini of cutting off some or all of the legs of their victims just beyond the coxae. Several reasons have been suggested for this behavior: (1) the wasp may feed at the wounds; (2) the spider may fit better in the cell; (3) the spider may be more easily carried. I suspect that (1) may have been the original reason, but that this preadapted them for (2) and (3). Most Auplopodini walk forward with their prey, which is held beneath the body (Fig. 3); this would scarcely be possible unless the legs had been first cut off.

Perhaps more data have accumulated on the method of transportation than on any other phase of the biology, except perhaps nest construction. All Pompilidae use the mandibles in holding the prey, and most of them drag or carry the prey over the ground. Some species make short flights interspersed with ground-carriage, while others may fly considerable distances. Species which fly with the prey often drag it up a tree or some other high object before taking off; this is true of some species of *Poecilopompilus* (Belt, 1874, pp. 133–134) and *Sericopompilus* (Krombein, 1953*a*, and observations of writer). *Anoplius depressipes* Banks preys on large semiaquatic spiders of the genus *Dolomedes* and flies over the water dragging the spider across the surface film (Evans, 1949). Those species which employ ground transportation may grasp the spider in various parts of the body and move either backward or forward. The most common habit is to grasp the spider by the base of the hind legs and to drag it backward, anterior end up, the abdomen and legs of the spider more or less dragging on the ground. A great many Pompilini exhibit this behavior, for example, *Anoplius apiculatus* (Smith) (Fig. 1). This species, when carrying a small spider, is quite able to reverse itself and run forward. The species of *Calicurgus* seem always to walk forward. *Sericopompilus apicalis* (Say), which has been observed on several occasions by the author, always grasps the spider by the extreme front of the cephalothorax and drags it venter-up, walking backward (Fig. 2) or flying from high objects with the spider dangling from its mandibles. Most Auplopodini walk forward carrying the spider beneath them, the spider's legs having previously been amputated; the spider is commonly grasped by the spinnerets (Fig. 3). Nearly all pompilids grasp the spider by the spinnerets when pulling it into the nest. Iwata (1942, p. 54) presents interesting data on the relative weight of wasp and spider for several examples, and points out that since the spider nearly always weighs more than the wasp, and sometimes several times as much, the available methods of transportation are few as compared with those available to wasps of other families which use several small prey per cell rather than a single large one.

During transportation, the prey is usually deposited at intervals while the wasp explores ahead. Some species leave the



FIGS. 1–3. 1. *Anoplius apiculatus autumnalis* (Banks) dragging its spider, *Arctosa littoralis* (Hentz). 2. *Sericopompilus apicalis* (Say) dragging its spider, *Paraphidippus chrysis* (Walck.). 3. *Auplopus* sp. carrying its spider, *Trachelas tranquillus* (Hentz).

prey at random on the ground, while others conceal it in various ways. The Peckhams (1898, pp. 126–138) found that *Episyron quinquenotatus* (Say) frequently suspends the spider in the crotch of a plant, and Krombein (1953*a*) observed this habit in *E. biguttatus* (Fabricius). *Pompilus plumbeus* Fabricius often buries the prey temporarily in a shallow hole while it investigates the terrain or the burrow (Richards and Hamm, 1939, p. 76).

There are many differences among various spider wasps in the manner of *nest construction*, but this is almost a subject in itself and cannot be explored fully here. The mud-building Auplopodini are a particularly interesting group in this respect, and I cannot refrain from mentioning that one species of *Auplopus, mellipes* (Say), not infrequently takes over the abandoned nests of other wasps and reconstructs them to its own use, though quite able to build its own nest. The nests of the common mud-dauber (*Sceliphron*) are sometimes used, and in the U. S. National Museum there is a nest of a paper wasp (*Polistes*) which was taken over and patched up with mud by an *Auplopus mellipes*. A type of nest strikingly different from those of all other pompilids is built by members of the genus *Priochilus*. These wasps build their nests under bark and in various plant cavities, using bits of leaves which they skillfully manipulate to form the walls of the cell, much in the manner of leafcutter bees (Williams, 1928, pp. 141–142).

With respect to differences in *oviposition*, it can be stated rather certainly that each species lays its egg in a rather specific and constant position on the abdomen of the spider. Iwata (1942) has an excellent plate showing numerous spiders bearing the eggs of spider wasps. The case of *Anoplius semirufus* (Cresson) and *A. apiculatus* (Smith) is discussed on a later page. *Ceropales*, as mentioned earlier, inserts the egg into the book-lungs. Differences in *closing* can also be mentioned only briefly. Fossorial types usually bite or scrape the sand off the walls of the burrow or rake it from the outside and pound it down with the abdomen. When the burrow is filled, sand is brushed over the entrance to conceal it, and in some forms lumps of earth, sticks, or other objects may be carefully deposited over the filled burrow. *Dipogon*, which nests in various types of natural cavities, is said to gather spider webs by means of a paired set of bristles on the maxillae and to use these in closing the nest, although some species employ plant fibers, pulp, or mud for this purpose (Richards and Hamm, 1939, pp. 67–70; Iwata, 1939).

The preceding survey, incomplete though it is, may serve to suggest the

very great number of ethological characters which exist and which are available to the taxonomist working with this family (even though the Pompilidae are notoriously more homogeneous in their behavior than, for example, the Sphecidae). The question may then be legitimately asked: have workers in this family availed themselves of these characters? The answer is yes and no. Certainly there has been an increasing awareness of the importance of biological studies as shedding light on relationships. Numerous authors have used behavioral characters to support or to question the existing classification. Yet the classification of the family remains largely a morphological one. Personally I feel that some aspects of the present classification are highly unsatisfactory, and that too great a reliance on structure has led us down a number of blind alleys, where we are deceived by convergences and blinded by unreasonable devotion to a few structural minutiae. I wish that I could present a new classification to prove my point; but the fact is that not nearly enough reliable ethological data are available at this time. The ethological systematist is now approximately in the position of the morphological systematist in pre-Linnaean times. He is in need of basic terms and techniques, and most of all he is in need of descriptive studies of the innate behavior of innumerable species. For only when we have reasonably detailed accounts of the behavior of many species can we begin to make deductions with respect to the higher categories. And only when enough workers are sufficiently impressed with the possibilities in this field can we really begin to exploit those possibilities.

Yet there are those who, even in reasonably well-studied groups, devote their energies to the search for further structural minutiae which will enable them to make "new species" *ad infinitum,* all the while under the illusion that to describe a species is to "know" it. These individuals would be appalled at the thought of spending several days watching a single common species, when they might be filling their cyanide jars with potential new ones. They would question, too, whether closely related species actually differ psychologically as they do morphologically. Personally I am convinced that they do, but that rarely do we have sufficiently detailed studies of individual species to make this clear. Such papers as those of Crane (1941), Spieth (1947), Fulton (1952), and others cited in the introduction, bear this out. Recently an excellent opportunity has arisen for comparing the behavior of two closely related species of the pompilid genus *Anoplius,* and the results of this comparison provide further corroboration. It is my hope that careful biological studies will eventually enable students of the Pompilidae to clarify a number of difficult complexes of closely related species.

An Ethological Comparison of Two Closely Related Species of Anoplius

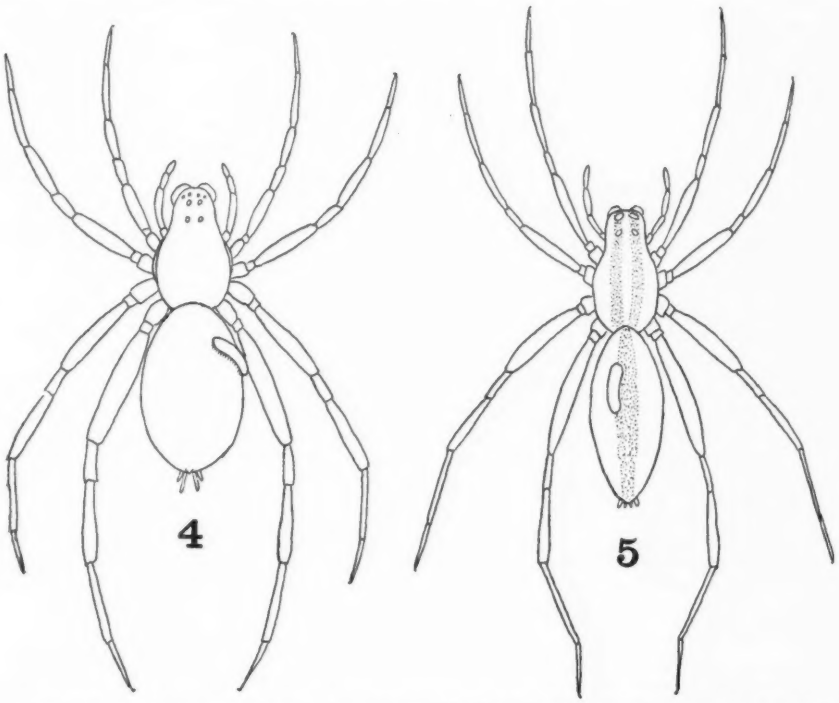
Anoplius semirufus (Cresson) and *A. apiculatus* (Smith) are two very similar species which until recently were much confused. Both are widely distributed in North America and both are restricted to sandy areas, particularly along watercourses. They may be separated morphologically by slight differences in the structure of the head and mesopleura of the female and by a slight difference in the shape of the subgenital plate of the male. In his recent revision of this group, the present writer (1951*a*) assigned these two species to the subgenus *Arachnophroctonus* of the genus *Anoplius* and placed them in a special species-group. *A. semirufus* is monotypic, but *apiculatus* is divisible into three subspecies on the basis of color and pubescence of the female.

A few years ago nothing was known about the biology of either of these species. By a curious coincidence, both K. V. Krombein and the present writer, working independently several hundred miles apart, have recently been able to study both these species in some detail. Krom-

bein worked with *semirufus* and with *apiculatus pretiosus* (Banks) at Kill Devil Hills, near Nags Head, North Carolina, in the summer of 1950 (reported in Krombein, 1953*a*) and again in 1952 (Krombein, 1953*b*). The writer and his assistants worked with *semirufus* and with *apiculatus autumnalis* (Banks) during 1952 at Blackjack Creek, Pottawatomie County, Kansas. Our studies of the latter form have been reported in some detail (Evans, Lin, and Yoshimoto, 1953) but those of *semirufus* have not been published. The striking similarities between Krombein's observations and ours clearly demonstrate the ethological discreteness of these two species. The following notes represent a summary of our combined observations; for the sake of brevity Krombein's observations are indicated by KVK, and those of the author and his assistants by HEE.

The similarities between these two species are many; in numerous details of behavior (as of structure) they are nearly identical. The following twelve ethological characteristics appear to be shared by the two species. (1) Both nest in areas of bare sand having a relatively high water table. (2) Both belong to ethological type VPTIOC. (3) Both prey on spiders of the family Lycosidae. (4) Both carry the spider by walking backward, grasping the spider by the hind coxae, the anterior end of the spider up (Fig. 1). (5) The manner of digging and filling the burrow is virtually identical in the two species. (6) In both species the burrow is at a slight angle from the perpendicular and of approximately the same depth (4 to 17 cm., averaging about 10 cm.). (7) The spider is dragged into the nest by the spinnerets. (8) The spider is packed tightly into the cell, which is only slightly wider than the burrow itself. (9) The spider recovers promptly from the effects of the sting, usually within a few hours. (10) The egg stage requires about two days, the larval stage five or six (only five for the combined egg and larval stages in one specimen of *apiculatus* reared by KVK). (11) Both species spend roughly three weeks in the cocoon. (12) Both breed continually throughout the summer.

After this formidable array of similarities, one may well ask whether they differ at all. However, several distinct and important differences are apparent from the data which are now available. (1) Although both species nest in bare sand, often in close proximity, *semirufus* leaves the open sand and enters woods or scrubby areas to do its hunting. The spiders preyed upon by this species are those characteristic of leaf litter or heavy vegetation: *Schizocosa crassipes* (Walck.), *S. saltatrix* (Hentz), *Lycosa punctulata* (Hentz) [KVK], and *L. rabida* (Walck.) [HEE]. In sharp contrast, *apiculatus* does its hunting on open sand, preying exclusively on *Arctosa littoralis* (Hentz), which it flushes from shallow holes in the sand. This is confirmed by four records from North Carolina [KVK] and numerous records from Kansas [HEE]. Thus these two species are by no means competitors for their prey. (2) During hunting, the wings of *semirufus* are folded flat over the abdomen [KVK] and during nesting activities they are held rather stiffly above the thorax [KVK, HEE]. On the other hand, *apiculatus* vibrates the wings constantly during all of its activities [KVK, HEE]. (3) While digging the nest, *semirufus* leaves the spider from 4 to 15 inches away, either on the sand (2 records by KVK, 2 by HEE) or on the leaf of a plant (2 records by KVK). On the other hand, *apiculatus* leaves the spider just outside the burrow entrance, where it usually becomes covered with sand [KVK, HEE] or actually inside the mouth of the burrow [HEE]; in either case it is reasonably well hidden. It has been suggested that this habit of *apiculatus* may be an adaptation for minimizing robbery by others of the same species or parasitism by miltogrammine flies [HEE]. With reference to the latter, however, it was found that *apiculatus* in North Carolina was much troubled by miltogram-



FIGS. 4–5. 4. *Arctosa littoralis* (Hentz) bearing the egg of *Anoplius apiculatus autumnalis* (Banks). 5. *Lycosa rabida* (Walck.) bearing the egg of *Anoplius semirufus* (Banks).

mines while *semirufus* was not [KVK]. (4) The egg of *semirufus* is laid longitudinally on the dorsum of the abdomen (Fig. 5) [3 records by KVK, 2 by HEE], while that of *apiculatus* is laid obliquely and laterally near the front of the abdomen (Fig. 4) [15 records by HEE, 3 by KVK]. (5) Adults of *semirufus* have not been observed to feed upon spiders, but they do visit flowers for nectar. They have been recorded as visiting *Daucus carota* and *Chaerophyllum teinturieri* (Evans, 1951*a*); during the summer of 1952 I took one female on the flowers of *Lepidium densiflorum* and a series of females on *Euphorbia marginata.* I have also taken this species on honeydew. *A. apiculatus* has never been taken on flowers, but the females are known to feed upon spiders [HEE]. Krombein has taken both sexes of *apiculatus pretiosus* on oak foliage, where they were presumably seeking honeydew.

Until further studies are made of these two species in other areas, it would be rash to assume that all these differences are completely valid. I suspect, however, that if some fall others will become apparent. It is worth pointing out that while one would be hard put to discover any adaptive value in the minor structural differences which separate these species, this is much less true in the case of the behavioral characters. While an accurate ethological diagnosis of a species is extremely difficult to arrive at, it gives one a far better basis for deductions concerning the origin and relationships of that species. Innate behavior patterns have certainly played a major role in the evolution of most groups of animals, and in so far as they are associated with certain

structures, probably preceded those structures in origin. To my mind the great amount of work necessary to characterize fully the behavior of a species is more than justified by the value of the information obtained.

Discussion

The above conclusions respecting *Anoplius semirufus* and *A. apiculatus* were based on a study of a considerable number of specimens in their natural habitat in two widely separated localities. Any weaknesses in the conclusions are due to the fact that insufficient specimens from too few localities were studied. The necessity of working with a *series* of specimens is even greater here than in comparative morphology. Not only must one deal with individual variation, which is probably no greater or less than in the case of structural characters, but also with *plasticity* of behavior. Plasticity is, in effect, intra-individual variation. While an adult animal can never change its structure, except perhaps through wear or injury, its behavior is undergoing constant change to meet varying conditions of the environment. Since the environment is never exactly the same from one moment to the next, it is perfectly correct to say that no animal ever acts exactly the same way twice. This is the reason why observations of a series are so much more valuable than observations of a single individual: only then can one begin to perceive the underlying core of inherited behavior patterns. One must also be in a position to rule out, or at least fully understand, modifications of behavior as a result of experience (see Thorpe, 1950).

Comparative ethologists may feel fortunate that so much progress has been made in recent years toward a more precise understanding of the nature of innate behavior. The word "instinct" has been stripped of its mystical overtones and has come to represent a biological concept about which a great body of research, both observational and experimental, is arising. The work of Lorenz (1937, 1941, 1950) is of the utmost importance, and Tinbergen's recent book *The Study of Instinct* (1951) is a veritable handbook for ethologists. Thorpe's brief paper "The Modern Concept of Instinctive Behaviour" (1948) provides a notably lucid and concise view of present understanding of this phenomenon.

I particularly like Thorpe's figure of speech (apparently first used by von Holst) when he describes instinct as being "finely adjusted to the exact details of the environment by the coat of reflexes governed by exteroceptive stimuli." It is in this "coat of reflexes" that individual variation, plasticity, and learning are most evident. It is essential that the comparative ethologist remove (but not discard) this "coat of reflexes' by observational work on many individuals and in different areas, or by experimental work wherever feasible. For it is the underlying core of instinct that is innate and genetically controlled; here is the proper milieu of the systematist.

Lorenz (1950) suggests that the animal behaviorists and the systematists have at last found a common ground, such as the morphologists and systematists have had for many decades. That common ground is comparative ethology, which promises to contribute as much to the one science as to the other. This is a rich field, and one which is likely, in the long run, to lure many a taxonomist from the comfort of his desk and the reassurance of his orderly arrays of dried specimens. Perhaps the day is approaching when systematic zoologists will become students of animals rather than students of corpses and skeletons.

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Taxonomic Recognition of Variation in Opiliones

CLARENCE J. and MARIE L. GOODNIGHT

HOW much variation should be allowed within a single species is a matter of major concern to the systematist. Such has not always been the case. Not too many years ago the main problem was simply that of naming the animals within one's sphere of interest. A new species was not a rarity, and the worker's chief task was that of defining these unknown forms. He was but little concerned with the problems of variation and evolution. Our present task is much more difficult. The modern worker has not only the problem of recognizing new species, but also that of evaluating the old and new ones and fitting them into a scheme which will show their interrelationships. To do this adequately, he must recognize the significance of the findings of evolution, genetics, and ecology for the interpretation of his problems.

Though most taxonomists are fully aware of these facts, many have failed to incorporate the knowledge into their work. While acknowledging evolution, their descriptions of numerous species seem more to verify the theory of special creation and the fixity of species!

In the study of a taxonomic group, the systematist must begin with an extension and, if possible, a verification of earlier investigations. More often than not, it soon becomes apparent that the first descriptions were made with complete disregard of possible variations, and that the apparent order is really disorder. Even though the higher categories may be correctly delineated, the generic and specific definitions may require a complete revision. As greater numbers of specimens become available for study, it is possible to determine how much variation may occur within a single breeding population. As these variations are studied, it becomes clear that each genus or even species must be investigated individually; for, while the principles of evolution, genetics, and ecological variation are universally true, their details vary within each group.

The end result of such a study is often a drastic reduction in the number of recognized genera and species. This is particularly true for animals exhibiting a high degree of variability which have been intensively investigated by early workers. This is a far different achievement from that usually attributed to systematists by scientists not engaged in taxonomic work. Too often these latter have believed that the sole aim of the systematist was that of immortalizing his name by placing it behind numerous specific names.

In most groups, the problem of the present-day taxonomist is essentially an integrative one. To do his work adequately, he must assemble large collections, study the animals individually, investigate their ecology, and then define his species in the light of our present dynamic concepts of speciation. Frequently, as pointed out above, the result is a drastic reduction, rather than multiplication of the total number of recognized species and genera. While this method of study greatly increases the difficulty of the taxonomist's task, it does make his contribution much more valuable to the general biologist. Taxonomic data then become an integral part of our advancing knowledge of biological phenomena.

To the present writers, these problems are particularly pertinent, for the opiliones have been a favored group for uncritical study.

The Order Opiliones

The order Opiliones is one of the numerous orders of the class Arachnida. The members of this order are quite varied in general appearance, size, and structural details. They have been divided into three suborders: the Cyphophthalmi, Laniatores, and Palpatores.

Of these, the cyphophthalmids are the least numerous. They are mite-like forms of secretive habit whose distribution and ecology are but poorly known. They are most numerous in the Mediterranean area, Africa, southeast Asia, and New Zealand. Of the New World species, two are known from the Pacific Northwest (Oregon and Washington), one from Florida, and three from South America. Cyphophthalmids are characterized by paired elevations which bear the scent glands, and by the absence of a genital operculum.

The laniatores are widely distributed throughout the subtropical and tropical regions of the world. In the neotropical region they are the most abundant representatives of this order and may be encountered in nearly all types of habitats. However, only a few species range northward into the United States. Several families have been erected within this group. In the New World, these include the families Cosmetidae, Phalangodidae, Triaenonychidae, and Gonyleptidae. The members of this suborder are characterized by the presence of a genital operculum, a heavy palpus with a well-developed claw, and the tarsi of the third and fourth legs either with double claws or with single ones bearing lateral projections.

The third suborder, the Palpatores, is abundant throughout the world. It includes the commonest species encountered in the United States and Europe. These opiliones are characterized by the presence of a genital operculum, small palpi which are without a claw or with only a small one, and the tarsi of the third and fourth legs with single claws without lateral projections.

So abundant are the long-legged palpatores in late summer that they were recognized by the European peasants as being distinct from spiders. Their scientific classification began with Linnaeus's recognition of certain common European species. Once explorations had begun in the New World, the handsome, large tropical species were eagerly collected by the early travelers and sent back to interested scientists in Europe. Many different arachnologists participated in the rapidly enlarging knowledge of this abundant group. In 1923, Roewer published *Die Weberknechte der Erde*, in which he summarized the knowledge acquired up to that time.

While the fine work done by many of these earlier workers cannot be discounted, they were all handicapped by the fact that they invariably had only a few specimens of each form, usually from only one locality. Furthermore, few had the opportunity to study the tropical species in the field and to combine their museum studies with observation of the living animal in its environment.

As a consequence of this lack of adequate material, a great number of species and genera have been erected. Both species and genera have been defined on the basis of color pattern, dorsal spination, leg spination, tarsal numbers, and various structural details. Studies in the field and analyses of large populations have indicated that all these characters are subject to considerable variation. Thus, while species and even genera may be based on these characters, each form must be studied and analyzed in much larger numbers from many populations. In almost every case where this has been done, the result has been to reduce a number of species into population variants and subspecific groups.

Field investigations have demonstrated that the majority of these opiliones are vigorous, wide-ranging forms, and it is reasonable that much variation should be encountered and that many species should be divisible into subspecific groups or races. While these observations apply to

the majority of species, there are still some small forms which have narrow ranges. These are usually found in mountain valleys or tops, caves, or other specialized and isolated habitats. It is among this group that new species are still to be found in some numbers.

Only by extensive collections and field studies can the range of a particular species be determined. As is to be expected, most of the better-known species are of the vigorous, wide-ranging type. It is among these that the variations have been uncritically used to set up numerous species and monotypic genera.

In our recent study of the opiliones of Chiapas, Mexico, and adjacent areas, we were able to demonstrate that the above conclusions did have a basis of fact. It was clearly shown that the generic and specific definitions as determined by earlier workers were based on inadequate understanding of variations. By careful study of long series of phalangodids, we reduced the number of recognized genera in Mexico and nearby areas of Central America from approximately fifty to eight. Even more astonishing were the results of such analysis with the cosmetids. Three well-defined genera adequately contained an assemblage of 64 ill-defined ones.

Some highly variable species were definitely shown to have been described numerous times under several different generic and specific names. *Cynorta clavotibialis* (Cambridge), for example, has been known under at least five specific and three generic names.

Observed Variations

As mentioned above, minor variations in color pattern, palpal spination, dorsal spination, leg spination, number of tarsal segments, and other structural details have all been used to define species and even genera among the opiliones. A brief consideration of some of these characters will provide some information as to their relative importance.

Color variation. In some instances, intensity of color has been used to separate supposedly different species. The difference in degree of color may involve the entire body or perhaps only the appendages. Enough studies have now been made of these color variations to demonstrate conclusively that this character cannot be relied upon to define species. More nearly adequate collections have, in all cases studied, indicated that the darker individuals were melanistic phases or members of melanistic races. With sufficiently extensive collections, all degrees of intermediates are demonstrable.

Homolophus biceps (Thorell), for example, shows an interesting series of body colorations, varying from light to dark. This species ranges along the Rocky Mountains from southern Canada to Arizona and New Mexico. Among the northern forms, the entire animal, especially the palpi, is quite light; among the southern ones, the body and palpi are much darker. When the extremes are contrasted, the difference is striking, but specimens collected from intermediate areas show varying degrees of this melanistic tendency. With sufficient material, a cline can be clearly demonstrated.

Among the phalangodids of the species *Bishopella laciniosa* (Crosby and Bishop), specimens from Tennessee, Alabama, and Georgia are light reddish-brown in color; however, the specimens from northern Florida are very dark reddish-brown, some being nearly black. On the basis of insufficient collections, this melanistic phase was first considered a separate species (*Bishopella marianna* Goodnight and Goodnight).

Color pattern variation. The members of the family Cosmetidae (suborder Laniatores) ordinarily have elaborate yellow or white patterns on the dorsum. These patterns stand out vividly against the reddish background, and have frequently been used to separate species. While it is true that the general form of the pattern is a valid specific character, great variation must be allowed. Previous workers have

not recognized this, and have separated many species on the basis of such minor differences as the presence or absence of white fleckings. When sufficiently large numbers of individuals are studied, great variability is discovered.

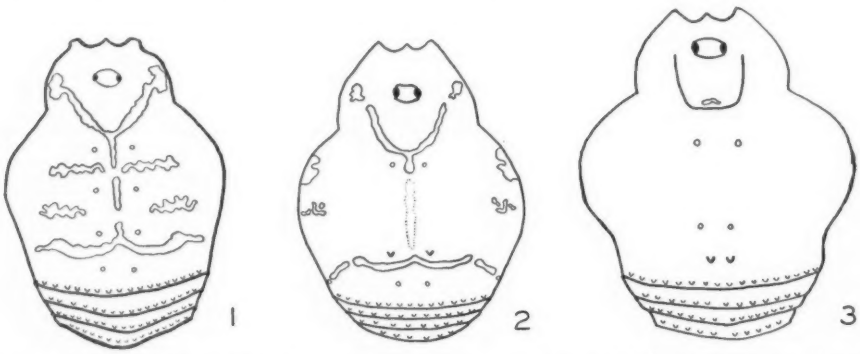
A good example of this variability is found in the cosmetid *Libitiodes ornata* (Wood) (Figs. 1–3). This species ranges from Florida into Texas, and from the Gulf States northward to southern Illinois, Indiana, and Ohio. The Florida specimens have an elaborate white color pattern, while those from Texas often lack all vestiges of white markings. These have been recognized as different species, but the error of this conclusion is shown by a study of specimens from Mississippi or other intermediate regions. Many of these animals have a color pattern vaguely similar to the Florida specimens, but very much reduced. In short, this represents only a cline with different populations and, at the most, geographical subspecies.

In the high mountains near Las Casas, Chiapas, Mexico, the most abundant cosmetid is *Cynorta casa* Goodnight and Goodnight. Most specimens have fine broken white lines which vaguely outline the first three areas of the dorsum and indicate the median line. Some specimens, however, have more white than others, and a few lack white markings entirely. This range of variation can be found in a single collection from a single area.

Many similar examples could be cited. In species with more elaborate patterns, the amount of variation may be even greater, though the general form of the pattern will hold for nearly all specimens.

Dorsal spination. Most members of the suborder Laniatores have a variety of combinations of spines and tubercles on the areas of the dorsum, the free tergites, and on the anal operculum. The arrangement of the armature has been used to define not only species but also genera. While again it is true that the pattern of the spines and tubercles is a valid character to use for the designation of species, much variation must be admitted. So great are the variations that only in rare instances can they be used for generic characters.

In a long series of the cosmetid *Vonones incrassatus* (Cambridge) from Chiapas, Mexico, dorsal spination was found to be exceptionally variable. One specimen from southeastern Chiapas had paired spines on both the third and fourth areas, while most others had spines only on the third. On some individuals even these spines were reduced to tubercles, and a few specimens lacked spines even on the third area. This is not a population dif-



FIGS. 1–3. Color pattern variation of dorsum among males of *Libitiodes ornata* (Wood). 1. Male from Hatchet Creek, Coosa County, Alabama. 2. Male from Hattiesburg, Mississippi. 3. Male from Austin, Texas.

ference, but only an individual variation, since all variants may be found in a single large series.

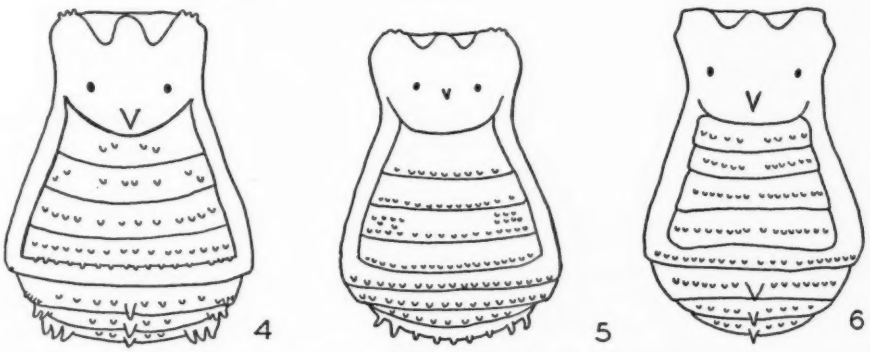
Cynortina acanthotibialis Goodnight and Goodnight, a member of the subfamily Phalangodinae of the Phalangodidae showed similar variation. From one collection in the mountains of southeastern Chiapas, most of the specimens had comparatively small spines on the free tergites and anal operculum, although one large male had the median spine of the anal operculum extremely elongated. By contrast, the males from a collection along the coast, which was just a few miles away, had heavy spinose tubercles on the free tergites and anal operculum.

Another phalangodid, *Stygnomma spinifera* (Packard) occurs in eastern Yucatan, Cuba, and southern Florida; the different populations may be divided into subspecies on the basis of dorsal spination (Figs. 4–6). The males of *S. spinifera spinifera* from Florida typically have median and lateral spines on each free tergite. *S. spinifera tancahensis* Goodnight and Goodnight from Quintano Roo, Mexico, lacks these spines but has small tubercles. *S. spinifera bolivari* (Goodnight and Goodnight) from Cuba has median spines on the free tergites, but lacks the lateral ones. Some overlap and variations between these geographical subspecies may be demonstrated from intermediate areas.

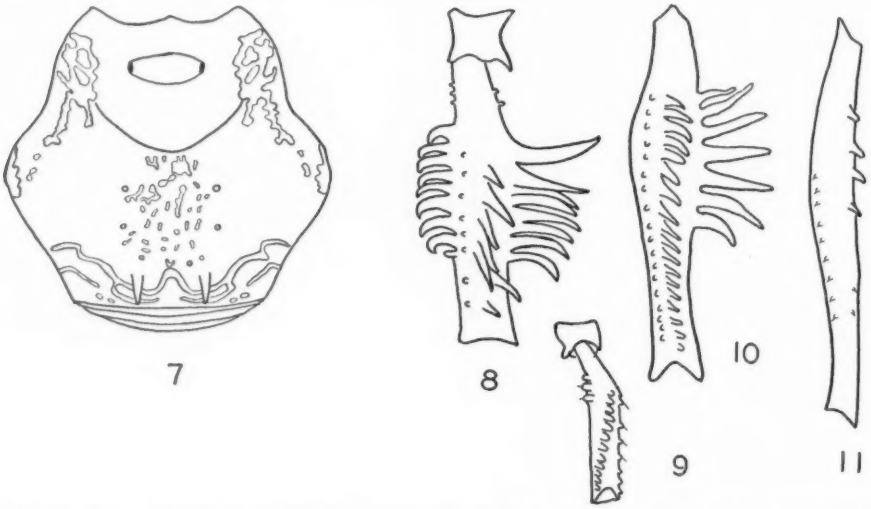
Another cosmetid, *Metacynortoides obscura* (Banks) from the West Indies presents a comparable situation. All the specimens studied had a row of tubercles across the fifth dorsal area; in some, however, the median pair of this row was enlarged into tubercles. In other individuals, the median tubercles were so slightly enlarged as not to suggest median armature.

Leg spination. The degree of incrassation of the third and fourth legs of the male has been used as a generic character. This character, however, is subject to great variation, and should not be used for distinguishing between genera. In those forms that have legs armed with spines, the details of these spines and their arrangement are of specific importance. Here again, much variation must be recognized.

Cynorta subserialis (Cambridge) (Figs. 7–11) ranges through southeastern Chiapas along the Pacific coast and up into the high mountains. Over the entire range, the dorsum as well as the general appearance of the animals is very similar; however, the leg spination is so variable that it is possible to recognize three subspecies. The fact that these populations are subspecies rather than distinct



FIGS. 4–6. Variation of dorsal spination among males of *Stygnomma spinifera* (Packard). 4. *S. spinifera spinifera* (Packard) from Royal Palm Hammock State Park, Florida. 5. *S. spinifera tancahensis* Goodnight and Goodnight from Touloum, Territory of Quintano Roo, Mexico. 6. *S. spinifera bolivari* (Goodnight and Goodnight) from Cueva del Cura, near Havana, Cuba.



FIGS. 7–11. Variation in leg spination of males of *Cynorta subserialis* (Cambridge). 7. Dorsal view of male. 8. *C. subserialis tricristatus* (Cambridge) from Cacaohuatan, Chiapas, Mexico. Ventral view of trochanter and femur of fourth leg of male. 9. *C. subserialis subserialis* (Cambridge) from Huehuetán, Chiapas, Mexico. Ventral view of trochanter and femur of fourth leg of male. 10. *C. subserialis gertschi* (Goodnight and Goodnight) from El Virgel, Chiapas, Mexico. Ventral view of femur of fourth leg of male. 11. *C. subserialis gertschi* from Tonalá, Chiapas, Mexico. Ventral view of femur of fourth leg of male.

species is clearly indicated by the presence of intermediate forms.

Great variation may also be found among animals from a single locality. In a study of a single collection of *Cynorta clavipes* (Cambridge) from Pichucalco, Chiapas, one male had extremely heavy spines, while others had no spines on the fourth femur but had a peculiar swelling on the distal portion of the fourth tibia.

Cynorta clavotibialis (Cambridge) had such extreme variation in its leg spination that it was described as two species by Cambridge (*Erginus clavotibialis* and *E. serratotibialis*). Studies of a single collection of animals from Jesus Carranza, Veracruz, Mexico, showed not only the spination described by Cambridge for his two species, but also intermediate forms.

Many similar situations could be cited, but these few will suffice to illustrate the problem. Leg spination is a valid character if studied sufficiently to establish the extent of possible variations. The definition of species based on minor differences of this character can only result in synonyms.

Tarsal segments. Among the laniatores, variation in tarsal segments has until recently been considered a valid generic character. A study of numerous specimens of many species reveals that only the first tarsus consistently has a certain number of segments. This, then, has value as a generic character. The combination of other tarsal segments is of specific value only if reasonable variation is allowed.

In some species, the number of tarsal segments is virtually constant, while in others it varies regularly. In some 200 specimens of the phalangodid *Pachylicus acutus* (Goodnight and Goodnight) which were carefully examined, only one single variation from the normal 3–7–5–5 count was encountered. The variation was minor; one specimen had eight segments in the second tarsus rather than seven. Yet this abundant species ranges throughout much of Chiapas, Tabasco, Veracruz,

Campeche, Oaxaca, Yucatan, and even into British Honduras. On the other hand, *Paramitraceras granulatus* Cambridge with a much more restricted range (the high mountains of Guatemala and Chiapas) had either three or four segments in the taxonomically important first tarsus.

The cosmetid *Vonones compressus* (Cambridge) is very abundant in Yucatan, Tabasco, Campeche, and Chiapas. The tarsal count of this species varies so widely that, with the older generic concepts, this form had been described under several different genera. In a single collection from Ocosingo, Chiapas, the tarsal count was found to be extremely variable. A few examples are as follows: 5–8–6–7, 5–10–7–7, 5–7–6–6, and 5–9–6–6. The only consistent feature was the presence of five segments in the first tarsus.

In a long series of *Vonones incrassatus* (Cambridge) from the Rio San Gregorio, Chiapas, three males had the following tarsal count: 5–9–6–7, 5–10–6–6, and 5–10–6–7. This last specimen even had six segments on one first tarsus and five on the other. Females from the same locality showed the same variation.

Among some gonyleptids, sexual variation in tarsal count has been found. According to the older generic concepts, this would place the males in one genus and the females in another.

Eye tubercle. The shape and armature of the eye tubercle of the phalangodids and gonyleptids are fairly constant and may be used as a specific character. Here again, variation is observable. In some species, paired spines may be present on the eye tubercle; in other individuals of the same species, these may be reduced to tubercles, and in others may be entirely lacking. There is also considerable sexual variation in this armature.

Summary

Numerous observations had indicated a need for a critical evaluation of the characters at present used for the definition of opilionid genera and species. Among the characters which have been used are color pattern, dorsal spination, leg spination, number of tarsal segments, and shape of eye tubercle. This study has shown that all of these are subject to considerable variation. Since the degree of variation has not been previously recognized, many genera and species have been incorrectly defined and the number of names enormously multiplied.

Each species must be studied individually, for each has its own range of variation for each of its characters. For such a study, it is necessary to have large collections from many different localities. Only in this way can a species be properly defined. Many areas must be adequately sampled, and this sampling must be correlated with the particular environmental conditions. This emphasizes the importance of the investigator's doing as much of his own field work as possible.

When all the facts concerning variation of characters are incorporated into a revised taxonomy of the opilionids, a classification is assured which is much more in line with modern concepts of genetics and evolution. This results in a drastic reduction of the number of genera, with those that remain showing more relationships and hence being more significant. Similarly, many described species are reduced to subspecies or synonyms. Many species are also demonstrated to be more wide-ranging than had previously been believed, and many are found to be developing into distinct subspecies.

While the present study has been confined to only one order of the arachnids, perhaps it indicates a need for similar studies among other groups of animals.

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(*Concluded on p. 192*)

Plant Taxonomy Today

REED C. ROLLINS

THERE has been a strong tendency toward introspection in our subject in recent years. More than once our leaders have felt impelled to examine the tenets we hold, our methods of inquiry, the fabric of the subject matter, and the theories that motivate our activities. The relationships of taxonomy to other branches of botany have been frequently reviewed. All this "self-inquiry" is healthy. It shows a willingness to extend, modify, or change ideas in conformity with new facts and logical conceptions. However, change for its own sake has no place in this; and those who seek to promote change for its novel aspects should be promptly opposed.

The rapid rise of genetics in the past fifty years has been variously received by taxonomists. Some have shown considerable suspicion of it. Others have gone so far as to give up taxonomy entirely to spend their whole time working in genetics. Actually, though not generally recognized in so many words, genetics has provided taxonomy with a very firm underpinning. From genetics has come an explanation for many things previously well known but unexplained in our field. More than any other branch of biology, it has provided a sound philosophical basis for our activities. The implications of the simple truism that "like begets like" are undoubtedly a very ancient observation of man. Today we can still say "like begets like" if we add "within broad limits" and "under most circumstances." The first qualification permits us to properly interpret "like" to mean "similar," not "identical." Thus we move from the special creationist idea to a modern viewpoint in which variation is recognized as the normal outcome of a reproducing population of plants. The second qualification permits us to take into account such phenomena as interspecific hybridization, aploploidy, and a variety of special genetical and cytological situations. Furthermore, we may allow for the accumulation of gene changes and the shifts in gene patterns that inevitably occur in breeding populations, as well as the introgression of genes from one species into another. Genetics has supplied the basis for these important qualifications. As a corollary to these established principles, it is perfectly evident that the variation that does occur, originating from a given reproducing genetic pattern, is not at random, and there is, therefore, a set of limits to this variation as well as a point at which some expressed phenotypic pattern within these limits reaches its highest frequency.

The Role of Intrinsic Factors

It should be stressed for our purposes that the most constant and basic characteristics of a given phenotype are the ultimate products of intrinsic factors consisting largely of the genes. Constant and relatively discrete phenotypic characteristics were first used to delineate the Mendelian principles of heredity. Similarly, it is upon these genetically controlled phenotypic characters that a sound classification must be built. Basically, we as taxonomists are interested in the phenotype as an expression of the genotype, not primarily in the genotype *per se* as some have claimed. It need not concern us so much that the relation between gene action and its ultimate phenotypic expression is exceedingly complex. Our attention is of necessity focused on the end-products rather than upon the way in which genes bring these into being. Taxonomic studies are ultimately concerned with whole individuals, groups of individuals, and finally various taxa. Analyses of the multitudinous parts and organs of an individual as to origin, structure, and

function are synthesized into an understanding of the whole. Further, the genetic history of individuals and the populations to which they belong provide the basis for considerable knowledge of the relationships of living taxa. Thus they may be viewed from the depth of time. Finally, we must study the present-day and past distributional patterns of species, for in such studies lie the answers to questions as to where they occur on the earth's crust today and where they have occurred in the past. The answers are relevant to an understanding of the species themselves. I am not oblivious of the fact that certain gene systems are involved in bringing about continuous variation, such as that of size. This type of variation is important in the classification of closely related groups and may be easily taken into account by methods designed to show the total range and greatest frequency of such variation.

The main points I wish to stress are that the major phenotypic characteristics of a living plant are considered to be validated expressions of the genotype, and in using them for taxonomic purposes, we are on the same ground as the geneticists who use them for genetic analyses. We are with good company and the ground would seem to be safe enough. But there are some pitfalls.

In emphasizing the genetic aspects of species differences, some workers have highlighted reproductive incompatibility, even going so far as to make this the sole criterion of species separation. The significance of this type of incompatibility in the evolution of distinct taxa on specific and infraspecific levels is unquestionable in certain groups, but its use as a supercriterion in setting species limits is certainly an untenable procedure. Reproductive incompatibility is not an all-or-none proposition in most instances and it does not arise from a single cause. At one extreme, similar types of incompatibility may exist between different members of the same population, at the other, between different species. Incompatibility is obviously most effective evolutionally when it is associated with other isolating mechanisms. Such isolation is presumably most frequent at the beginning of species differentiation, not an end-product of it. The importance of effective reproduction in breeding populations, which in turn make up races and taxa of higher order, is of course fully recognized.

The folly of using reproductive incompatibility as *the* criterion of species distinction has been ably dealt with by Gates (1951). He points out that to insist on infertility (incompatibility) as the sole criterion of species "ignores the aims and methods of taxonomy and seeks to make taxonomy subservient to a condition—sterility in genetics, by raising it to the importance of a universal principle."

The erroneous idea that species throughout the plant kingdom are essentially equivalents has led to attempts to discover universal criteria for distinguishing them and to construct definitions that will cover all organisms so grouped. To anyone who has worked extensively in taxonomy, it is obvious that species in different large groups are not equivalents. In most instances they are nowhere near equal. For this reason, a single species definition would seem to be an impossibility no matter how long and involved it was. But if the term species has a different connotation in different groups and it is impossible to define for universal application, then of what use is the word *species* and why do we use it so frequently? These are questions I should like to leave for the moment, to be taken up further on.

The Role of Extrinsic Factors

Our intended reliance mainly upon characters whose variation stems from the operation of intrinsic factors makes it necessary to distinguish between these and the characters whose variation is the result of change in the environment. Here lies one of the crucial problems in our subject. For a time, particularly under

the leadership of Bonnier (1920) and of Clements (1929), there was a strong environmentalist trend. Environmental factors were held to be of very great importance in molding the ultimate nature of a population and in many cases to outweigh intrinsic genetic factors in maintaining species differences. Today we see the expression of a different form of this notion in Lysenkoism. However, the contentions of Bonnier and of Clements, that one species can be converted into another merely by transplanting it from lowlands to high mountains, or vice versa, has been fully discredited by the brilliant work of Clausen, Keck and Heisey (1940, 1948), who point to the early work of Kerner (1891), with whom they agree. They have demonstrated repeatedly and conclusively that species characteristics, born of intrinsic factors, are relatively stable under radically different environmental conditions. Changes that do occur purely in response to the environment are reversible, giving no indications of permanence. They report that "some of these changes in vegetative characters are quite spectacular, yet they never obscure the individuality of the plant, which is retained irrespective of the conditions of altitude, light, and moisture in which the plant is grown." I am sure you are all familiar with these studies and the conclusions derived from them.

Assuming that all of us will not have available the extensive garden facilities that are needed to determine experimentally the nature of the variation in given populations, we are often required to attack our problems in a different way. When this is necessary, we may fall short of the ideal. However, in all instances we should carry our studies as far as facilities and materials will permit. Students, particularly, should be encouraged to utilize every means at their disposal to make the results of their studies as nearly perfect as possible.

It has long been known that the overall dimensions of the plant-body and its vegetative parts are sensitive to external influences. Because of this, we have the axiom in plant taxonomy that qualitative differences in the vegetative body are more significant for classificatory purposes than are quantitative differences. Furthermore, structures maturing decisively at an early stage in the formation of vegetative parts are less subject to environmental influences than those with a prolonged formative period. For example, most trichomes when present on the leaves of Angiosperms, mature and the cells lose their living contents at a very early stage in leaf development. For this reason, they are far less apt to vary quantitatively due to extrinsic factors than the leaves themselves.

Though dealing with the whole plant, we select for special attention features reflecting most accurately its hereditary constitution. The reproductive parts and associated structures are in general less sensitive to environmental influences than the vegetative portions of the plant (Anderson, 1929; Turrill, 1936). Here, relatively large quantitative differences are more likely to be significant than in the vegetative structures. But again, greatest emphasis for taxonomic purposes is placed upon the qualitative aspects of the structures involved. Polyploidy and the frequently associated size-effects in many plants are too well known to be ignored.

The Role of the Herbarium

We have heard a good deal in taxonomy recently about the study of dynamic populations, of natural hybridization, of introgression, of gene ecology, of apomixis. These modern aspects of some of our problems are popular, and studies involving them carry an implication of *right*. From them we stand to gain a more penetrating understanding of various plant groups and their biological nature. Unfortunately, accompanying increased activities along these lines one finds a tendency to deprecate "specimens," and hence the herbarium, and for that matter, classical taxonomy comes in for its share of punishment.

For a moment, I should like to say a little about the role of the herbarium in taxonomy. Actually, we have in it a unique method of documentation. Specimens so placed are relatively permanent and are scarcely subject to manipulation to obscure the facts they reveal. In them, investigators for centuries have available, as nearly as one could hope for, exactly the same basic materials. The specimens should be looked upon as samples. As such, they may be studied in a wide variety of ways. They are samples of the taxonomic groups to which they belong; of a particular flora; of a plant association; of a specific population; of a particular combination of morphological and anatomical characters; and of the product of a particular set of genes. Whether any set of specimens fully represents a given taxon obviously depends upon the circumstances. It is doubtful whether any herbarium has specimens showing the complete variations of more than a few species, if even one. However, one good specimen is concrete evidence that a particular taxon exists or has existed, and considerable information can be obtained from it. It is self-evident that the amount of information obtainable does not double when a second specimen of the same taxon is acquired. The amount from each new specimen of a representative series will never equal that obtainable from the first. For this reason, the extent and kind of specimen-representation in a particular herbarium will depend largely upon its objectives and facilities. Perhaps it would be ideal to have the total variation of all taxa represented by specimens in some herbarium, but such a goal is impossible of achievement. Merely to determine the total range of morphological variation of a given taxon, using all the means and methods available, is practically an impossibility, let alone having it represented in an herbarium. Assuming the latter were possible, continuous evolutionary changes would often make such a representation obsolete. This type of natural limitation is not confined to the taxonomic side of things but is equally operative in other branches of botany. The problem of adequate samples is ever present. However, considerable communicable knowledge concerning various taxa can be assembled and a lot can be represented by specimens in the herbarium. It is to the possible that we direct our attention.

The system of arranging specimens in an herbarium is impressive. The availability of any one of the one million three hundred thousand specimens in the Gray Herbarium never ceases to be a marvel to me. Our specimens are far more accessible than the books in a large library. The key to the arrangement is the system of nomenclature which of necessity places the specimens under species names. Our esteemed friend and former president, Dr. Camp (1951), seems to feel that such a procedure leads many taxonomists to regard the *specimens* so placed as the *species*. Perhaps such a tendency exists, but it is hard to imagine a more satisfactory way of doing the job. Personally, I have never met a taxonomist who would argue that a species resided in a museum case. Representatives or samples of a species, yes, but not the species. When I climb to the twelve-thousand-foot level on Hoosier Ridge in Colorado and see individuals of a certain mustard growing among the rocks, I may pick up a plant of it and remark that it is *Draba crassa*. But I do not delude myself into thinking that that particular plant is the species, for I know there are thousands of individuals on Hoosier Ridge, not to mention the tens of thousands on the other peaks of the Colorado Rockies. Rather, the plant I held in my hand was a sample of *Draba crassa*. One might, in like manner, contemplate a particularly vigorous Jack Pine in northern New England, and suddenly exclaim "Why this is *Pinus Banksiana*." He would not thereby declare that particular tree to be *the species*, for he would know there are hundreds of thousands of living trees of Jack Pine to be found anywhere from Quebec to Saskatchewan. We work by sampling in the field

as surely as we do in the herbarium, and both have the natural limitations inherent in the technique. I doubt whether anyone is capable of a full comprehension of the diversity represented in all the individuals of a single populous species.

The Role of Experiments [1]

There is a popular notion that the real and the only way to get at the true nature of a given taxon is to go at it experimentally. Bring the plants or their offspring into the experimental garden where they can be manipulated in accordance with our best-planned experimental procedures. The results, when properly codified, tell us considerable, but for taxonomic purposes it is often in the nature of additive information to that obtained in other ways, and rarely replaces or negates it. Personally, I believe the more experimentation designed to reveal the nature of species and other taxa the better, but experimental taxonomy is not the whole answer to the problems in our subject. Experimentation is beset with limitations, as are all methods of investigation, and this we must recognize. In the first place, experiments must be carried out by using samples and they are, therefore, subject to the natural limitations of sampling techniques. Secondly, it is next to impossible to sample most taxa adequately. In my own experience, forty acres of experimental plantings were wholly inadequate to provide a proper overall sample of *Parthenium argentatum,* a species comparatively restricted in its geographic range. How many of us have forty acres available for experimental purposes?

It seems almost redundant to say that critical observation and study in the herbarium alone, in the field alone, in the experimental plots alone, or in the laboratory alone, are insufficient for the realization of the primary objectives of taxonomy. A combined attack, using to the fullest the techniques of all these, will scarcely be sufficient to complete the job, but we should get closer to our goal using all of them than we would by using but one. If, in addition, we borrow as much information from other branches of botany as is pertinent and possible, we should proceed a step further toward our ultimate goal. Thus viewed, taxonomy becomes an integrative and synthesizing subject, in a way rising on the shoulders of its sister disciplines.

[1] It is not my purpose to develop this subject in the manner that might be implied from the present heading, for to do so would occupy my entire time.

What Is a Species?

One of the stumbling blocks upon which the introspective wanderer inevitably barks his shins is the precise definition of terms. Whether we like it or not, the precise meanings of many scientific terms begin to be altered immediately after they have been proposed. After a few generations have been at work their meaning has often been altered completely. As ideas and ways of looking at subject matter change, the meanings of applicable words are shaded to accommodate the new view. Shifts in meaning are usually so gradual and so closely tied in with the current of contemporary communication, that they frequently go unrecognized until considerable difference from the original has developed. The words we have the most trouble with are those closely associated with changing concepts. For example, to the pre-evolutionists the term species was definite enough. The immutability of its meaning was immediately upset by the concepts of evolution and its preciseness was further devalued by the impact of genetics. Now we are told that no one knows what a species is, and that perhaps there isn't any such thing anyway. Yet anyone who has dealt with whole organisms, whether plant or animal, complex or simple, is fully aware of certain patterns of populations that are reproduced with fidelity over great periods of time. He knows with certainty that at a given time level, the

members of neither the plant nor the animal kingdom represent a continuum, no matter what the vantage point from which they may be viewed. Given the facts that organismal diversity exists and that it does not exist in a continuum, the taxonomist's job is to assemble and systematize a body of communicable knowledge about the different kinds of the earth's plants, both of the present and of the past, that will reveal their true nature. In this, the problem of species remains a major one in spite of all that has been said or written upon it. I dare not venture a guess as to the number of times the species problem has been discussed. Certainly it is a perennial of many years' standing and it appears to grow more lustily as the years go by. It seems generally agreed among most discussants and writers that a universally applicable species definition is a must and that without it taxonomy lacks the dignity of a science. Some have viewed the problem of defining the term species as a futile one, others lifted the problem to a light vein by suggesting that species are completely subjective and are what a good taxonomist says they are. In taxonomic literature, we even see descriptions of new concepts instead of new species.

Since *species* is one of the key words in our subject, we shall continue to be badgered by questions for an explanation of it. There has often been a certain amount of irrationality in the way of coming to complete grips with the problem. We have sought to satisfy the philosopher-logician type of inquiry by trying to provide a definition of the term. Naturally, others would like to know what we mean when we speak of a species, whether it be of an alga, a conifer, or a mint. But I think none of us have really believed that the curious could find out on their own what a species was in any one of these groups by using our numerous and varied definitions. Even the incompatibility test, which perhaps came as close to being practical as any, brought forth only negative evidence in many instances. If two particular plants of presumably different species would not cross and produce fertile offspring, one could never be sure that two other plants representing different strains of the same two presumed species would behave similarly. In specific groups where authorities supposedly held the secret as to what the species were, there were always intangibles and indefinable somethings that aided in species determination. I do not minimize the necessity of knowing a group nor of diligent attention to every possible detail. The point is, the species definitions we have concocted are not practical. I happen not to agree with most of the attempted dispositions of the problem of determining what species are, and, for this reason, feel somewhat justified in speaking about it. Certainly the problem is very much with us and still needs attention.

In the first place, I should like to state my unqualified belief that there are species in nature quite apart from man's contemplation of them. It is not necessary to call them species, but there are groups of closely interrelated organisms that reproduce themselves with a surprising fidelity over long periods of time—and I am thinking now in terms of millions of years. These species are not equivalents in different large plant groups and, considering the tremendous diversity in the plant kingdom as a whole, it would be surprising if they were. The species in relatively unrelated groups do not have the same attributes, they did not arise in the same way, and they most probably have been subjected to a wholly different combination of environmental influences during their phylogenetic life. Why, then, should we be surprised that a universal species definition for them seems impossible? I do not agree with the notion that because we do not have a satisfactory man-made species definition, the whole fabric of taxonomy comes crashing down around our ears. The species are not man-made. The difficulty arises from trying to pour into a single kind of mold the thousands of almost totally different kinds of

plants all will agree are represented in the plant kingdom. The problem is one of interpretation. But why try to produce a universal definition? Why not let the species themselves tell the story? In order to elucidate this latter question I must start with some basic facts.

Genetics has provided us with a valid principle upon which to build. This may be stated as follows. The closer the genetic relationship of individuals or groups of individuals, the greater the number of genes they have in common. Conversely, the more distantly related, the fewer common genes. Remembering the specificity of gene action, it is obvious that similar or identical genes and gene systems produce similar end-products. Thus we are justified in using the phenotype as an indicator of relationship. If, as we must assume, similar genes provoke similar organizational patterns, then it follows that genetic variation is controlled in a like manner. Indeed, this has been shown many times. Here is the crucial point, providing the basis for taxonomic use of the organizational pattern of an individual as well as the variation of such a pattern that may be found among all the individuals making up a species. It is in the area of variation that we have learned most in recent years. From the main principle springs the logical basis for the comparative method.

How distant may the relationship be of two groups of plants and there still remain common gene lineages that will operate to produce detectable specific similarities in the phenotype? This we do not know, and there is no organized information on the point. However, parallel variations and changes have been repeatedly observed in species known to be related. It is no stretch at all to suppose that the species of any given genus, or at least subgenus, have numerous common genes and, therefore, we can expect similar characteristics, similar patterns of variation, similar modes of genetic change and even similar responses to external factors. That such is actually the case in many genera can readily be shown. Similarities of this sort permit us to extrapolate from one species to related species. Between certain closely related genera there must also be a community of genes and gene patterns. The species most difficult to distinguish, using all types of criteria, are the most closely related. These have been the source of greatest consternation because of the difficulty of knowing where to draw the line between such species and infraspecific taxa. "Where does the species stop and the subspecies or variety begin?" is the question frequently asked. How many different genes must two populations of plants possess before they are species? How many similar genes may they possess and remain on the species level? These are pertinent questions, but they cannot be answered for the vast majority of cases in which they may be asked. Our present knowledge of most plants is much too fragmentary to provide exact answers. But if we should ask how many and what type of different phenotypic expressions of genes are required before a group of like plants are a species, or only part of a species, there is a way of providing the answer. This way is based upon the expected similarities of related species as mentioned previously and the use of comparative procedures.

The Species-standard Method

For the present, let us focus our attention upon the so-called difficult genus *Arabis* of the Cruciferae. It is not an extremely large genus, having roughly 65 species in North America and a few less in the rest of the world. Nor is it small as genera of Angiosperms go. Within it are complexes of species difficult to interpret and separate. Polyploidy is present and interspecific hybridization occurs. At least one species is apomictic (Böcher, 1951), and the rest have not been studied from this point of view. But there are also perfectly distinct, well-characterized species in the genus, too. Often they have distinctive geographic ranges. These dis-

tinct species are obviously so, to any discerning taxonomist, and one could obtain complete agreement among botanists willing to study them more than superficially. When I worked on *Arabis* as it occurs in western North America some years ago (Rollins, 1941), I studied these well-defined species in as much detail as possible at that time. They provided the basis for interpreting the more difficult series. They were biological standards of comparison, so to speak, that revealed in themselves what a species is in *Arabis*. There was no need for arbitrary species criteria nor man-made definitions. To have used them would have obscured the facts as revealed by these clearly defined species. In this study, the species used as standards were *Arabis blepharophylla, A. cobrensis, A. Crandallii, A. crucisetosa, A. Cusickii, A. dispar, A. furcata, A. glaucovalvula, A. Koehleri, A. Parishii, A. perennans, A. platysperma, A. rectissima, A. Schockleyi* and *A. suffrutescens*. Among them are representatives of all four groups or series of species of *Arabis* occurring in the area. Some of the species are widespread, others are restricted geographically. Some showed less variation than others. In all cases the patterns of variation were of the same general type. Similarly, the same pattern of definitive characteristics ran through the entire group. While the species-standards, individually and collectively, were the real key to species interpretation in the whole genus, certain working hypotheses as to the value of particular characteristics emerged from a study of them. For example, the presence or absence of trichomes on the leaves and stems of *Arabis* was found to be an unreliable criterion of species difference. On the other hand, qualitative differences in the trichomes proved to be of considerable value.

The method used to determine "what is a species?" in *Arabis* is one partially used by many monographers, though in most instances it is not done in an organized way. It is my conviction that an extension of the method is highly desirable and would go a long way toward solving the practical aspects of the "species problem." The use of biological standards of comparison is an accepted procedure in other branches of botany. The *Avena* coleoptile test, the *Staphylococcus aureus* test for penicillin concentration, and the growth-rate test of chemical concentration in *Neurospora*, to mention only a few, all depend upon a completely biological standard. Many biological stains and reagents are standardized by purely biological tests. In numerous instances, whole organisms are involved whose complete development is no more controlled nor in fact known than are the wild plants with which we work. The use of living and dead plant samples in formulating species-standards and the use of these in determining the species of a given group, is vastly more complicated than the tests mentioned above. But the method is sufficiently extensible to meet our requirements.

What are the possibilities and ramifications of the species-standard method? Perhaps this can best be shown by assuming that we are setting about to determine "what is a species?" in a hypothetical genus. First we study our materials sufficiently to be able to select for intensive investigations those species that are readily discernible. These materials may be specimens in the herbarium, populations of plants in the field, or plots of them in the experimental garden. In a well-kept herbarium having a reasonable representation of the genus, this step will have been largely done. In many herbaria, the specimens will reflect the cumulative wisdom of a number of workers who have studied them. Study of the geographical ranges of distribution often aids materially in this first stage. I anticipate that someone will say at this point that there are some genera in which there are no clear-cut, easily recognized species. Personally, I do not know of a single genus in which such species may not be found. Certainly the notoriously "difficult" genera *Poa, Salix, Rubus, Crataegus,* and

Hieracium have readily distinguishable species that might be utilized for our purposes. Naturally, it is necessary to exercise some judgement in the selection of these species and the competence of botanists will vary in this regard. But the critical aspects of the selection are so unrefined as to be within the scope of all who are trained. Furthermore, botanists outside of taxonomy with any acquaintance with its aims and methods will find the selection easy to follow.

The second step in our inquiry involves the detailed study of the selected species. Ideally, this should extend all the way from a careful analysis of the characteristics of a representative series of specimens to transplant work in the experimental garden. Data concerning the range of variation of the species in the field and under manipulated or selected environmental conditions should be gathered and processed. The morphology, anatomy, and cytology should be worked out with a view toward deriving usable information for taxonomic purposes. The reproductive cycle and mode of pollination should be studied. In short, these selected species should be subjected to the most thorough-going study possible. That is the ideal. Actually, most taxonomic studies will fall short of this ideal, except in a limited number of cases. But until such studies are made throughout the plant kingdom, our work is not finished. From this point of view, it is evident that we have scarcely started on the job ahead. The successful application of the method is not dependent upon any particular level of refinement or thoroughness of study of either the species-standards or the other species of a genus under consideration. The most accurate and reliable results will come from complete studies using wholly adequate materials. Where only the minimum of specimens is available and there is no opportunity to carry out experimental or field studies, the method can still be used with considerable probability of arriving at the proper species designations.

The method I have briefly outlined to determine "what is a species?" has several aspects that tend to clear the path of the logical impasse often cited in considering the species question. (1) It is free from arbitrarily selected criteria. Under this scheme, incompatibility or any other characteristic may be significant or insignificant, depending upon the group involved. (2) A universal definition is not required. The species are probably of a different sort in every major group. By recognizing this, we recognize the very great organic diversity existing in nature. Furthermore, we recognize the numerous ways in which species arise and the variety of circumstances under which they survive. (3) Species so defined are not a subjective creation nor a mere concept of man. However, a high percentage of agreement of interpretation should be possible. It should be clear that the species exist, independent of man's ability to define them or to perceive their presence. The fact that many species have reproduced themselves with fidelity for millions of years is ample proof of this (Stebbins, 1950). (4) The method is logical and largely objective, depending not on judgement alone but utilizing the best procedures in scientific research. Naturally, some judgement is required. No matter what is often claimed, there is a certain amount of subjectivity in all kinds of scientific inquiry. If this were not the case, neither ours nor other sciences would have any real meaning to man. (5) The method is extremely flexible, providing the procedure for determining the species in all groups, in such a way that it can be followed by anyone with sufficient training and interest. (6) It permits the assembly of an almost unlimited body of knowledge about determinable and redeterminable kinds of plants. This knowledge thus becomes communicable and the basis for its organization on a large scale is provided. This I consider to be one of the major aims of taxonomy.

How critical is the species-standard method? Simply answered, one might say

that the method is as critical as the time and energy of the botanist making the study will permit. The implication is that there are unlimited possibilities for the study of the species providing the standards of comparison within a given genus. This is equally true of the more difficult species that are dependent upon the use of these standards for their detection. The accuracy of the comparative procedures used for the latter purpose is dependent upon the precision and extent of the various comparisons made. Certainly, accuracy cannot be achieved without great care. Complexity stems from the complex nature of the organism itself and perhaps can never be avoided in taxonomy. As stated before, we deal in whole organisms, but the studies employed ordinarily involve analytical procedures in which any part of the plant may be the subject of attack. Such analyses may range from studies of chromosome behavior to the gross morphology of the flower. In the end, the results of analytical studies are synthesized into a body of knowledge that forms the basis for making appropriate comparisons.

As a general observation, it seems to me that taxonomy fails to appeal to some scientists because it does concern itself primarily with whole organisms, which are by their very nature exceedingly complex. Chemistry, physics, and astronomy have influenced all of science in the direction of desiring a one-to-one relationship between cause and effect. The nicety of mathematical precision has been a constant goal in the reduction of observation and experiment. More recently, these sciences have dealt with variable systems and the very complex relationships of various phenomena have been widely recognized. In spite of this reversal, the trend in many branches of biology has continued in the old path. On the whole, the struggle of biologists to simplify the interpretations of phenomena of living organisms has not met with spectacular results, but the directional emphasis has remained. As taxonomists, we find ourselves well outside the main stream of this activity because of the nature of our subject. Simplification cannot logically be carried below the complexity inherent in the living individual and the population of which it is a part. I do not say that analytical methods of all sorts may not be used to delve below this level, for it is extremely important that we utilize them to the utmost, but the information thus obtained, to be relevant, must be applicable to the plants as a whole. We are thus dependent upon information obtained largely by analytical methods, but in its ultimate, usable form it has to be synthesized into a whole. We are dealing largely with variables, and the complexity of the ultimate systems represented by the living individual, the population, and the taxon considered in time, is so much greater than known physical systems that there is no real basis for comparisons between them.

What would be the consequences of the widespread use of the method I have outlined? If the taxonomists who have described hundreds of apomicts in *Hieracium* had used it, certainly they could not logically have named them as species. It would have been absurd for me to have named as species fifty to a hundred apomicts in *Parthenium,* and I am convinced that the wholesale naming of apomicts as species, wherever they are found, is equally absurd. Babcock and Stebbins (1938), using the sexual species of *Crepis* as reference points for the organization of the apomicts in that genus, were certainly on the right track. I believe that the method would even permit agreement as to the numbers of species of *Rubus* or *Crataegus* in eastern North America. Perhaps I am unduly optimistic here, but I should like to see it given a trial.

Using the species-standard method, it would be impossible to recognize so-called cryptic species which show no morphological singularity even though they were incompatible with morphologically similar plants. But I do not believe these are, in reality, species. Difference in chromosome

number alone would scarcely be sufficient to set two species apart unless that were the rule throughout the genus. It would not help particularly in dealing taxonomically with species-hybrids and cases of introgression. However, many instances otherwise not easily seen might be detected. It is impossible to foresee the total ramifications of the wide adoption of such a procedure. It does throw emphasis toward the monographic type of study rather than the floristic, for determining what the species are to begin with. Such a procedure has long been recognized as desirable. The taxonomist, working with a particular flora without adequate reference to monographic studies, is indeed handicapped in arriving at natural specific boundaries. The danger of misinterpretations, when a single species or only a few species of a genus are studied independently, should be immediately apparent.

The two novel aspects of the proposed method are (1) the complete abandonment of any attempted species definition that would be of universal application, (2) the definition of species at a relatively low hierarchical level in the plant kingdom, i.e., probably most frequently within the genus. Thus a paradox of long-standing would be resolved. These are fairly radical deviations from the most common present-day ideas, so that one may ask how these changes would affect traditional taxonomy as well as the newer approaches to the subject.

In the practice of traditional taxonomy these changes should result in considerable improvement. Definite reference points within genera could be set up that would have real meaning to a wider audience of botanists. Greater agreement in interpreting difficult genera should be achieved and a more systematic determination of the species in generic revisions should result. Nomenclature does not enter, except as new interpretations call for nomenclatural adjustments. Insofar as the newer approaches to taxonomy are concerned, such as those developing in cytogenetics, experimental taxonomy, and the like, these would be as relevant as before and perhaps more so, for the information obtained could be brought more directly to bear on the practical problem of species interpretation. Thus, an integration of the old and the new in taxonomy might be envisaged for the ultimate benefit of us all.

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Zoologists will find that these sage observations on plant taxonomy apply as cogently to that of animals. The species-standard method herein described merits wide application. **REED C. ROLLINS**, Director of the Gray Herbarium, Harvard University, delivered this paper as his presidential address before the American Society of Plant Taxonomists, September 11, 1951. Reprinted from *Rhodora*, January 1952.

Points of View

Uniform Endings and the Revival of Interest in Taxonomy

The American Society of Ichthyologists and Herpetologists deserves well of zoologists generally for endorsing the proposal of Stenzel to use uniform endings for ordinal and familial names. As Hubbs truly says (SYSTEMATIC ZOOLOGY, *1*:146–147, 1952), "Stenzel's proposal is so alluring in its simplicity, consistency, and logic as to inspire, on first thought, agreement and adoption."

The advantages of uniform endings not just for students but for workers in every field of biological science from physiology to economic zoology would certainly be most welcome. In fact it would be analogous to the move out of the confusing world of ounces, grains, pennyweights, drams, scruples, carats, pounds, short tons, and long tons into the logic and consistency of the metric system. It is entirely possible that such a move would benefit the whole science of taxonomy both because the system was inherently better and because it increased interest in taxonomy and respect for it on the part of the great majority of zoologists. Taxonomy has been too long neglected, and, in some quarters, despised and ridiculed. Failure to scrap an intricate and illogical terminology when a better one is available will increase neither the usefulness nor the good standing of our science.

The objection which raised second-thought doubts in the mind of Hubbs concerns a proposal that Stenzel did not actually make but which his examples seemed to imply. It was that the names of supergeneric categories should be formed from the stems of generic names. Were this done, then an adjective formed from any familial name that happened to be used also for the name of the order would lose its precise meaning. In the example used by Hubbs, the adjective "poeciliid" from the family Poeciliidae would lose its precision should the Haplomi, the order to which this family belongs, be called the Poeciliida. However, this could happen only in one family in each order, and even then it would not be necessary. If the order Haplomi should be spelled Haplomida, this difficulty would not arise. All that Stenzel's first proposal advocates is the ending of all ordinal names in -ida.

In his article "For and Against Uniform Endings in Zoological Nomenclature" (SYSTEMATIC ZOOLOGY, *1*:20–23, 1952) Simpson explicitly points out that the two propositions, uniform endings, and the formation of supergeneric names from generic names, are distinct and separate proposals. In fact, even in the present chaotic lack of system, it would be possible to form all supergeneric names from generic ones. The doubts of Simpson arise from the fear that once zoologists accept uniform endings it "may set up a chain reaction" leading to the formation of all ordinal names from generic ones. Birds are cited as a group where just such a presumably unfortunate train of events has occurred. The present writer is not sufficiently familiar with avian taxonomy to comment here except to say that more than one ornithologist has written of the perfection of avian systematics.

However that may be, Simpson continues by supposing that "general application of uniform endings to, say, orders would at once wipe out or render almost unrecognizable a great majority of time-honored ordinal names in wide or universal use." The transformation of Coleoptera into Scarabaeida is cited as an example of what to expect. All this is indeed a nightmare, but like most night-

mares it happily does not coincide with the inevitable. Coleoptera could even more easily be written Coleopterida. Simpson himself very sensibly suggests Carnivorida for Carnivora, and in a personal communication to him, Stenzel has suggested Primatida for Primates.

Perhaps there should have been a further explicit provision in Stenzel's original proposal, namely, that *the uniform endings should be used in connection with the presently accepted ordinal and familial names.* If such a provision be made, then the very understandable fears expressed by Hubbs and Simpson evaporate. A quick glance at a variety of orders taken more or less at random throughout the Animal Kingdom will serve to reassure the most skeptical that there are no grounds for fear that our familiar ordinal names will be "wiped out or rendered almost unrecognizable." Among insects the following changes would be indicated: Thysanura to Thysanurida, Orthoptera to Orthopterida, Ephemerida unchanged, Diptera to Dipterida, Anoplura to Anoplurida. Among the Protozoa: Amoebozoa to Amoebozoida, Radiolaria to Radiolarida, Holotricha to Holotrichida. Among Coelenterates: Milliporina to Milliporinida, Siphonophora to Siphonophorida, Gorgonacea to Gorgonaceida. Among Platyhelminthes: Acoela to Acoelida, Tricladida unchanged. Among Molluscs: Opisthobranchia to Opisthobranchida, Pulmonata to Pulmonatida. Among Vertebrates: Urodela to Urodelida or Caudata to Caudatida, Falconiformes to Falconida, Rodentia to Rodentida, and Lagomorpha to Lagomorphida.

It is difficult indeed to believe that changes such as these would cause confusion. On the contrary they would bring a highly desirable order into what is at present a most deplorable confusion. In the list just presented, which certainly represents but a tiny fraction of the extant orders, there are well over a dozen different endings, disregarding the word stems for the moment. Specifically, here are to be found orders ending in -ura, -ptera, -ida, -ozoa, -aria, -icha, -ina, -ora, -acea, -oela, -dela, -chia, -ata, -iformes, -tia, and -pha.

To bring such a change within the scope of the international rules of zoological nomenclature might well require some action by a regularly constituted body concerned with such matters. The need for such a reform is urgent and the time past due if taxonomy is to regain its rightful place among the zoological sciences.

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Variation and the Taxonomy of Opiliones

(*Concluded from p. 179*)

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Major articles should be from 1500 to 10,000 words in length. Discussion articles should not be over 400 words unless of very general interest. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

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